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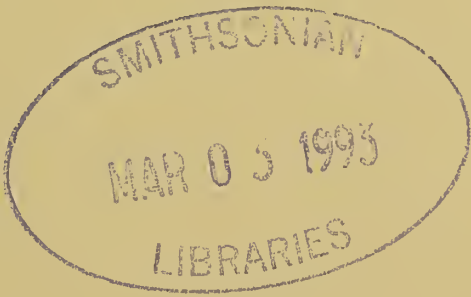
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SYSTEMATICS OF THE FALSE MAP TURTLES
(*GRAPTEMYS PSEUDOGEOGRAPHICA* COMPLEX:
REPTILIA, TESTUDINES, EMYDIDAE)

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ABSTRACT

Taxonomic relationships in the *Graptemys pseudogeographica* complex are reviewed and redefined. Variation of head pattern within clutches, within local populations and throughout the geographic ranges of the species were compared through canonical analysis. Environmental control of head pattern characters was confirmed by laboratory manipulation of incubation temperatures. Skeletons from specimens with known head patterns, and skulls from extremes in the geographic range, were used to show species separation and subspecies affinities. Canonical analysis of 37 morphological characters (including head pattern, shell and skull morphometrics) established differentiation of *G. pseudogeographica* and *G. ouachitensis*. Electrophoresis of plasma, hemoglobin, and muscle homogenate proteins showed little variation in 16 of 19 protein systems within populations, between populations of the same species, or between species. Malate dehydrogenase was the only polymorphic protein system. Analysis of courtship behavior showed that stereotypic displays of *G. ouachitensis* and *G. pseudogeographica* from sympatric populations are distinctly different. *Graptemys pseudogeographica* and *G. ouachitensis* are shown to be widely sympatric distinct species, each with two subspecies: *G. pseudogeographica pseudogeographica* and *G. pseudogeographica kohni*; *G. ouachitensis ouachitensis* and *G. ouachitensis sabinensis*. The allopatric *G. caglei* and *G. versa* are regarded as distinct, monotypic species.

INTRODUCTION

The false map turtle complex, including the nominal forms *Graptemys pseudogeographica*, *G. pseudogeographica ouachitensis*, *G. pseudogeographica sabinensis*, *G. kohni*, *G. versa*, and *G. caglei*, has long perplexed taxonomists. *Graptemys pseudogeographica* was described by Gray (1831) from specimens collected at New Harmony, Indiana, on the Wabash River. Baur (1890) described *G. kohni* from Louisiana specimens received from Gustave Kohn. Baur characterized *G. kohni* as having "a thin yellow line, which is connected with another one running behind from the upper part of the orbit." This trait was said to distinguish *G. kohni* from *G. pseudogeographica* with its large yellow spot behind the eye. Carr (1949) considered *G. kohni* a subspecies of *G. pseudogeographica*.

Graptemys pseudogeographica versa was described by Stejneger (1925) from the Colorado River near Austin, Texas. Smith (1946) elevated *versa* to species status. This species, which is geographically isolated from other *Graptemys*, is distinguished by a J-shaped mark extending posteriorly from the orbit and the absence of distinct vertebral knobs.

Cagle (1953) described *G. pseudogeographica sabinensis* and *G. pseudogeographica ouachitensis* from the southern United States. He stated that *G. pseudogeographica sabinensis* was restricted to the Sabine River in Louisiana and Texas, and that *G. pseudogeographica ouachitensis* occurred in the Ouachita River of

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Louisiana, but its range extended north and west into Texas, Oklahoma, Arkansas, and Kansas. Cagle proposed that *sabinensis* and *versa* were related on the basis of skull characters. He claimed that intergrades between the subspecies *ouachitensis* and *pseudogeographica* occurred in Indiana (UMMZ 89742, USNM 14669), Iowa (UMMZ 92691, 92692, 92696) and Tennessee (UMMZ 99230).

Cagle (1953) suggested three hypothetical relationships for species of this complex: (1) The narrow-headed forms (*G. pseudogeographica pseudogeographica*, *G. p. ouachitensis*, *G. p. sabinensis*, and *G. p. versa*) occupy mutually exclusive ranges and *G. kohni*, a wide-headed turtle, is a separate sympatric species related to *G. pulchra* and *G. barbouri* (the occurrence of apparent intermediates between *kohni* and *pseudogeographica* complicates this interpretation); (2) *Graptemys p. pseudogeographica* may be conspecific with *G. kohni*, whereas *versa*, *sabinensis*, and *ouachitensis* may be associated in a separate species group (in the South *sabinensis* occurs in sympatry with *kohni*, and farther north *ouachitensis* and *kohni* are sympatric, however Cagle noted this explanation did not account for the supposed intergradation between *ouachitensis* and *pseudogeographica*); (3) *Graptemys pseudogeographica* is a separate species and intermediates between it and the other named forms might be interspecific hybrids.

Later Cagle (1954), without explanation, treated *G. versa*, *G. kohni*, and *G. pseudogeographica* as distinct species, with the latter having three subspecies (*sabinensis*, *ouachitensis*, and *pseudogeographica*). This is the arrangement generally accepted in current literature.

Graptemys caglei was described by Haynes and McKown (1974). It was hypothesized that *G. caglei* was intermediate between *G. versa* and *G. kohni*, but judged by head pattern more closely allied to the latter species. Skull characteristics also suggested affinity of *G. caglei* with *G. kohni*, although females of *G. caglei* do not exhibit the wide-headed trait characteristic of some populations of *G. kohni*. *Graptemys caglei* was not compared with *G. p. pseudogeographica*, *G. p. ouachitensis*, or *G. p. sabinensis*. The most recent review of the systematics and relationships of the members of the false map turtle complex is that of McKown (1972). He found that starch gel electrophoresis of sera demonstrated no discrete differences between *G. pseudogeographica ouachitensis*, *G. p. sabinensis*, *G. versa*, *G. kohni*, and *G. caglei*. He placed *G. kohni* with the *G. pulchra*-*G. barbouri* group on the basis of head width. *Graptemys versa* and *G. caglei* were grouped together, and *G. p. sabinensis*, *G. p. ouachitensis*, and *G. p. pseudogeographica* were placed together. Even though no specimens of *G. p. pseudogeographica* were examined, he stated that "intergrades" between *G. pseudogeographica ouachitensis* and *G. p. pseudogeographica* from Missouri were analyzed.

Dundee (1974) presented data supporting the separation of *G. kohni* and *G. pseudogeographica ouachitensis*. He stated that the crescentic yellow post-orbital line is diagnostic for *G. kohni* and that, even if the crescent is disrupted by neck stripes, these stripes do not reach the orbit as in *G. p. ouachitensis*. He noted that in *G. p. ouachitensis* the postorbital yellow mark is reduced to a spot. Dundee also suggested that the "large-headedness" of *G. kohni* is diagnostic in separating that taxon from *G. p. ouachitensis*, as females over 100 mm carapace length and males over 80 mm carapace length were separated by the ratio of head width to carapace length. The much greater anterior projection of the frontal bones distinguishes skulls of *G. p. ouachitensis* and *G. p. sabinensis* from those of *G. kohni*, according to Dundee. Ernst and Barbour (1972) considered *G. caglei*, *G. kohni*, and *G. versa* monotypic species, and *G. pseudogeographica* polytypic with three

subspecies: *G. p. pseudogeographica*, *G. p. ouachitensis*, and *G. p. sabinensis*. In a more recent compilation (Ernst and Barbour, 1989) the same authors recognized *G. ouachitensis*, *G. pseudogeographica*, and *G. kohni*, along with *G. caglei* and *G. versa*, as distinct species.

I first became interested in the problem while attempting to identify Wisconsin turtles using the supposedly diagnostic head markings. The head markings of specimens collected from the Mississippi River near Stoddard, Vernon County, Wisconsin, suggested that several members of the complex occurred there sympatrically. Three possible explanations could account for the great range of head patterns in that area: (1) the variants are part of a single polymorphic species; (2) two or more species are present and their head pattern characteristics overlap; (3) two or more forms of a superspecies are present and intergradation, whether limited or extensive, has caused a confusing admixture of characteristics.

In 1971, I collected and incubated 26 clutches of eggs laid by false map turtles at Stoddard. Hatchlings with head markings reputedly characteristic of four different "taxa" emerged from these 26 clutches, in some cases multiple "taxa" coming from a single clutch. The characters of the hatchlings reinforced my first hypothesis, based on examination of adults in this population, that the four putative taxa, *G. p. pseudogeographica*, *G. p. kohni*, *G. p. ouachitensis*, and *G. p. sabinensis*, comprised a single highly polymorphic species. Smith (1961:150–151) suggested a similar explanation for variation observed in Illinois populations of false map turtles.

A study was begun in 1972 to determine the taxonomic relationships of the false map turtles at Stoddard. The principal study area, which has an unusually large population of *Graptemys*, extends northward 37.5 river km from a dam at Genoa, Vernon County, Wisconsin, to north of LaCrosse, Wisconsin (Vogt, 1980*b*).

I examined aspects of the ecology (Vogt, 1980*b*), courtship behavior, head and shell patterns, osteology, and protein characteristics in the Stoddard population. Preserved specimens from throughout the range of the complex were also examined. These were supplemented by additional collections from areas where samples were inadequate. Collections were made at 50–100 km intervals on the Mississippi, St. Croix, Chippewa, Black, and Wisconsin rivers in Wisconsin. In addition, a five-year laboratory study was conducted to determine growth rates, the effect of incubation temperature on sex determination (Bull and Vogt, 1979, 1981; Bull et al., 1982; Vogt and Bull, 1984) and head pattern inheritance, and ontogenetic change in head pattern.

METHODS

A collection of 1117 adult turtles was taken from the Stoddard study area. Turtles were captured in unbaited fyke nets using the techniques described by Vogt (1980*a*). Specimens were also obtained from the gill nets of commercial fishermen working in the area. For each specimen the following data were recorded: length, width, and height of carapace (to 0.5 mm); length and width of the plastron (to 0.5 mm); shell markings; weight; and sex. Dorsal, ventral, and both lateral surfaces of the head were photographed. The same data, exclusive of weight, were taken from over 2000 museum specimens (*see* Appendix 1).

Head photographs were taken at a standard distance and calibrated by photographing a metric ruler at the same distance. For analysis, a negative was projected onto a horizontal Tales Cybergraph tablet six times actual size. As each head spot or blotch was outlined with a stylus the outline appeared on a Tektronix

Graphics Display Keyboard, and was redrawn 15 times actual size. The outline was entered into a Harris 6024/5 computer which computed area, degree of circularity, and greatest diameter of each marking.

Thirteen characters of the head pattern of each specimen (Fig. 1) were quantified and compared at intra- and interspecific levels. Both discrete and continuous characters were examined. The discrete characters were the number of temporal lines entering the orbit and connection of the postorbital spots to the supratemporal lines. If a postorbital spot was connected to a supratemporal line a value of +1 was recorded; if not, a value of -1 was recorded. The two sides of the head were scored independently, and the sum of these two values for each specimen was treated as a single character. Thus values for this character were either -2, 0, or +2. The specimen in Fig. 1 has a value of $-1 + 1 = 0$. The number of temporal lines entering the orbit was recorded for each side of the head. If the postorbital and subocular spots were fused to form a complete crescent preventing temporal lines from entering the orbit, a value of -1 was given. If there was a space between the postorbital and subocular spots, but no lines entered the orbit, a value of 0 was given. The specimen in Fig. 1 has a value of 0 for this character for the illustrated right side of the head. Four of the continuous characters, the postorbital and mandibular spots, were measured twice from different aspects. This was done because these spots usually extended onto two head photographs. Part of each postorbital spot can be viewed from the dorsal aspect and part from lateral aspect. The mandibular spots were viewed from both the lateral and ventral aspects. Only rarely could the entirety of any of these spots be measured from one aspect. These characters were thus slightly weighted, since each occurs twice in a data set, but the area of each spot was never doubled by this process. The total area of the dorsal surface of the head was used as a covariate with pattern characters to negate the effect of overall size of the specimen. A total of 18 measurements was taken on the head pattern and shell of each specimen. The head markings of 558 turtles from 19 populations from throughout the range of the *G. pseudogeographica* complex were analyzed quantitatively (Table 1). When large series were available from a site, a sample of at least 20 was chosen at random for analysis. When possible, sites with large available samples of two or more forms in sympatry were chosen.

Separate canonical analyses (Seal, 1964) were performed on all continuous head pattern characters, on all head pattern characters, and on the head pattern characters and five shell measurements. A graph in which each individual is positioned according to the values of its first and second canonical variate shows variability within a population, and relationships between populations (Kowal et al., 1976; Kalunki, 1976). In addition, Mahalanobis' distance (1936) was calculated between all pairs of populations. This distance is measured in pooled, intra-population standard deviations and gives an index of separation between populations. For example, two populations separated by a Mahalanobis' distance of two overlap at one standard deviation from the mean, and 32% of the scores of one population

→
Fig. 1.—Dorsal, lateral, and ventral aspects of head pattern characters in the *Graptemys pseudogeographica* complex: 1—supratemporal lines; 2—right postorbital spot, dorsal aspect; 3—left postorbital spot, dorsal aspect; 4—sagittal stripe; 5—right postorbital spot, lateral aspect; 6—right subocular spot; 7—right mandibular spot, lateral aspect; 8—left postorbital spot, lateral aspect; 9—left subocular spot; 10—left mandibular spot, ventral aspect; 11—right mandibular spot, ventral aspect; 12—left mandibular spot, ventral aspect; 13—chin spot; 14—throat spot.

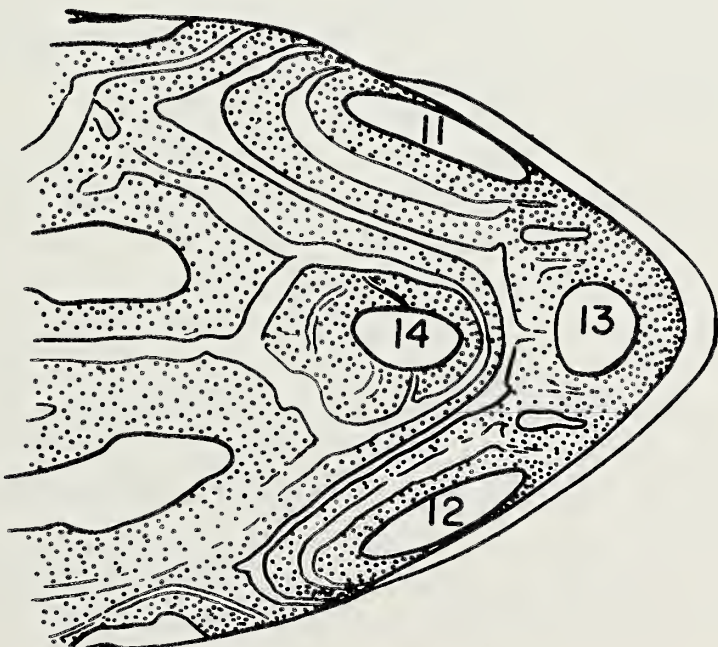
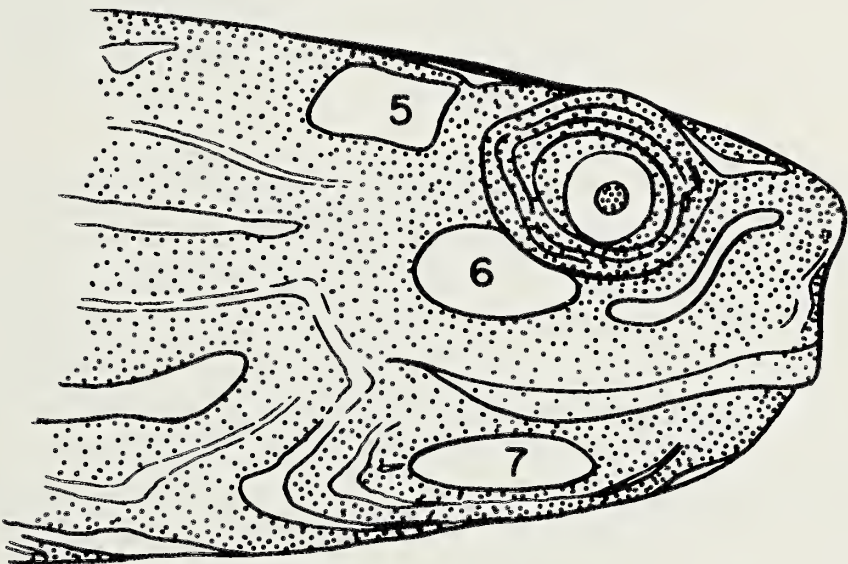
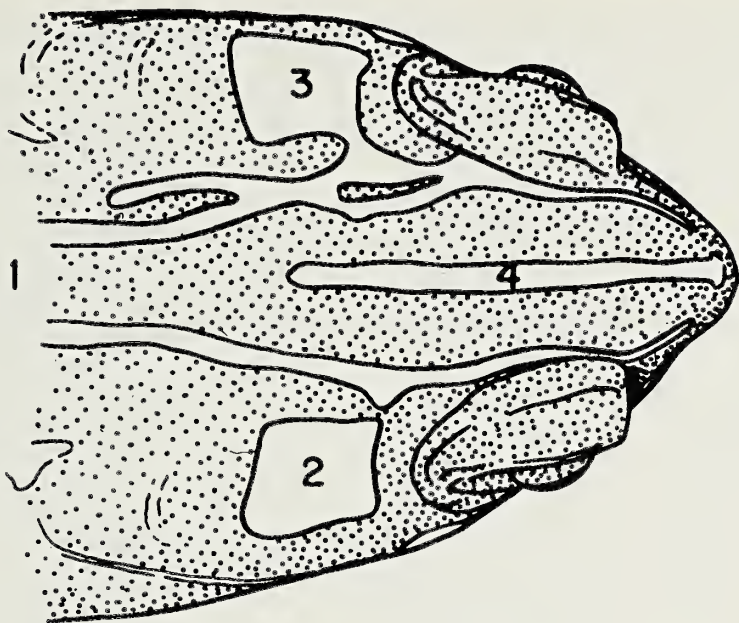


Table 1.—Population samples used in head pattern analysis.

Pop.	N	Species	Locality
1	135	<i>G. ouachitensis</i>	Wisconsin, Stoddard
2	26	<i>G. ouachitensis</i>	Illinois
3	11	<i>G. ouachitensis</i>	Indiana
4	9	<i>G. ouachitensis</i>	Tennessee and Kentucky
5	6	<i>G. ouachitensis</i>	West Virginia
6	19	<i>G. ouachitensis</i>	Arkansas
7	20	<i>G. ouachitensis</i>	Oklahoma
8	19	<i>G. ouachitensis</i>	Louisiana, Catahoula Parish
9	19	<i>G. ouachitensis</i>	Louisiana, Sabine River
10	119	<i>G. pseudogeographica</i>	Wisconsin, Stoddard
11	20	<i>G. pseudogeographica</i>	South Dakota
12	24	<i>G. pseudogeographica</i>	Illinois
13	8	<i>G. pseudogeographica</i>	Indiana and Ohio
14	21	<i>G. pseudogeographica</i>	Tennessee, Tiptonville
15	4	<i>G. pseudogeographica</i>	Kentucky
16	28	<i>G. pseudogeographica</i>	Tennessee, Reelfoot Lake
17	30	<i>G. pseudogeographica</i>	Arkansas, White River
18	20	<i>G. pseudogeographica</i>	Louisiana, Catahoula Parish
19	20	<i>G. pseudogeographica</i>	Louisiana, Sabine River

fall in the range of the second. A Mahalanobis' distance of six represents an overlap at three standard deviations and connotes less than a 1% range overlap.

Untransformed data with total dorsal head area used as a covariate gave better results than untransformed data without the covariate, or log-transformed data with or without the covariate. In canonical analysis, all characters potentially contribute to the Mahalanobis' distance between populations. The first and second canonical variates best depict the Mahalanobis' distances in two dimensions. Calculations were performed at the University of Wisconsin-Madison Computing Center on a UNIVAC 1110 computer using program CANCOV (Kowal, personal communication).

In 1972, 50 clutches of *Graptemys pseudogeographica* complex eggs of known maternal parentage (640 eggs) were collected from Stoddard and incubated in the laboratory. The head pattern characteristics were noted in the adults and recorded for the hatchlings. In addition, photographs were taken of carapace and plastron. The hatchlings were raised in the laboratory for five years as part of a study of differential growth rates between species and sexes (Vogt, 1980b), and changes in morphology and head patterns with aging were recorded.

In 1976 and 1977, 45 egg clutches were obtained by hormonal induction of oviposition (Ewert and Legler, 1978). Some eggs from each clutch in 1977 were incubated at 25°C, 30°C, and 35°C to study the effect of incubation temperature on head pattern inheritance and sex determination.

After their color patterns were recorded, 100 adults from Stoddard were skeletonized by dermestid beetles. Comparisons were made of the skull and shell morphometrics of *G. geographica* and *G. pseudogeographica* complex turtles from Stoddard and from the southern parts of the range. Skull (Fig. 2) and plastron measurements were taken with vernier calipers to the nearest 0.01 cm. Each character was measured independently three times; the mean of the three measurements was used for statistical analysis. Carapace measurements were taken with a device similar to that described by Cagle (1946).

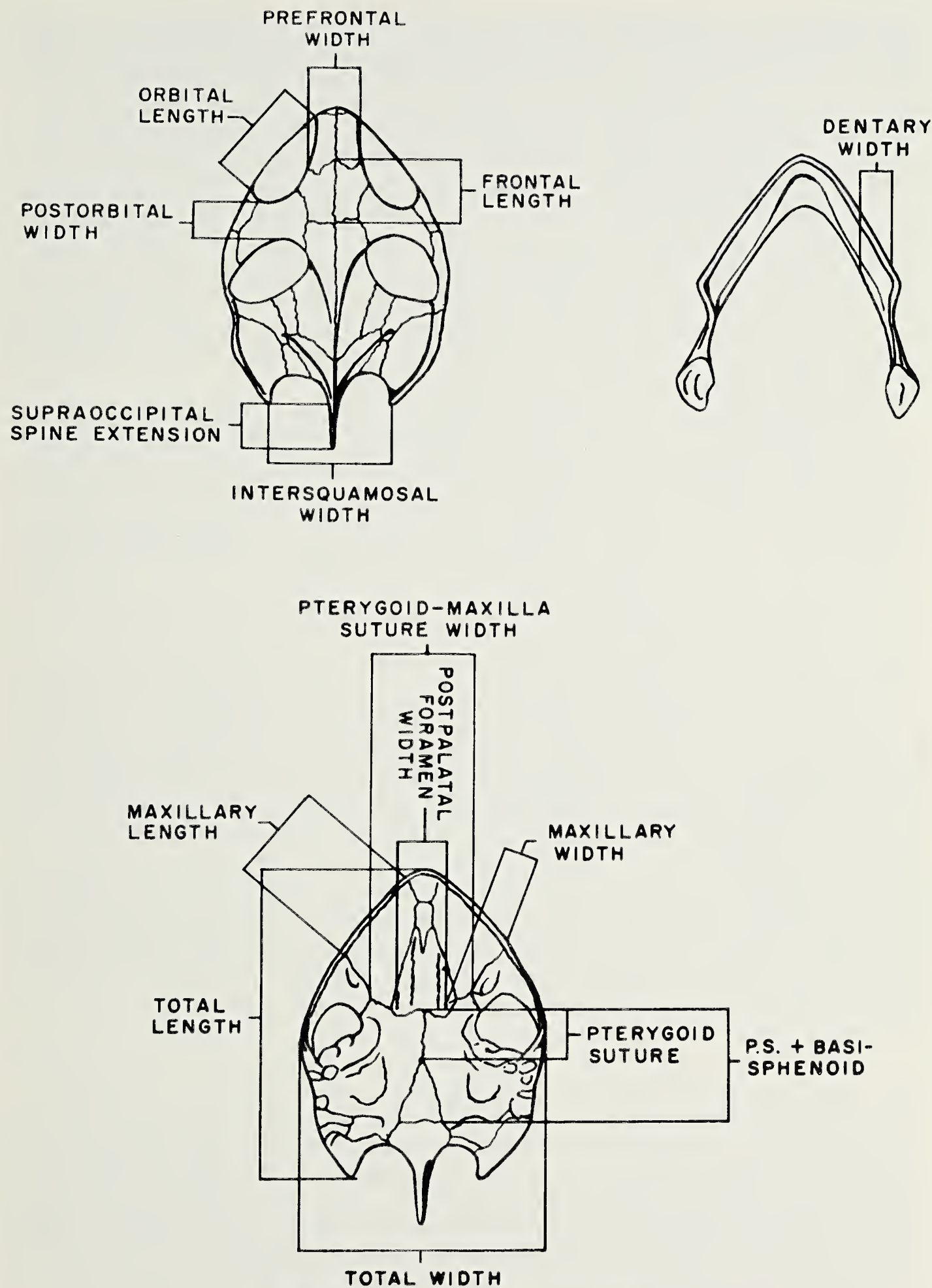


Fig. 2.—Diagram of skull measurements.

Horizontal starch gel electrophoresis was performed on plasma, hemolysate, and muscle homogenate. Blood was drawn into heparinized tubes by cardiac puncture, then centrifuged at about 10,000 G for 10 min. The plasma was drawn off and put on ice. Several drops of water were added to the remaining coagulated red blood cells and the tube vibrated for 2 min to lyse the red blood cells. This mixture was then centrifuged for 10 min at 10,000 G after which the supernatant was drawn off and placed on ice. Equal sized samples (1 cm³) of heart, liver, kidney, and striated muscle were removed and homogenized with an equal volume of 2% 2-phenoxy-ethanol. This homogenate was centrifuged at 10,000 G for 15 min and the liquid drawn off and placed on ice. Samples not tested within 1 hr were stored at -50°C. All voucher specimens were preserved and deposited at University of Wisconsin Zoological Museum-Madison or Carnegie Museum of Natural History. Tissue samples were deposited in the frozen tissue collection of Thomas Uzzel at the University of Illinois-Urbana.

The protein systems examined were: muscle, plasma, and hemolysate general protein (M-GP, P-GP, H-GP); muscle lactate dehydrogenases (LDH-1, LDH-2, LDH-3); muscle malate dehydrogenases (MDH-1, MDH-2, MDH-3); muscle glutamate oxaloacetate transaminase (GOT-2); hemolysate esterase (H-EST); plasma esterase (P-EST); hemolysate inhibition with esserine (H-ESS); hemolysate peptidase (PEP-1, PEP-2, PEP-3); plasma peptidase (PPEP-1, PPEP-2); and plasma leucine aminopeptidase (LAP). Electrophoretic techniques, stains, and buffers were similar to those used by Selander et al. (1971). Muscle proteins were examined using Tris-citrate buffer (Buffer 5) at 100 V for 4 hr. Hemolysate proteins were separated on the Tris-HCl buffer (Buffer 1) at 250 V for 1½ hr. Plasma proteins were run on lithium hydroxide buffer (Buffer 2) at 350 V for 3½ hr. The gels were stained and then photographed (Panatomic X). Mobility calibration of each sample was made by comparison to a standard, *Chrysemys picta belli*, run at three different places on each gel. The migration distance of the *Chrysemys* was assigned 1 and the other samples adjusted to this scale. Species or populations being compared were placed in alternate slots on each gel to negate possible differences in gel homogeneity.

The courtship behavior of *G. pseudogeographica* complex turtles from Stoddard was filmed in the laboratory with a Bolex 16 mm camera on Kodak Ektachrome VHF film at 24 and 64 frames per second. Films were made from both the vertical and horizontal aspects. Frame by frame analysis of male courtship films was made with a L. W. International photo-optical data analyzer.

RESULTS

Head Pattern

Variation in head patterns at Stoddard.—Despite the extreme variability of head pattern characters, quantitative analysis was performed to determine if species could be distinguished by head pattern, and if so, which features of the head pattern were responsible. Characters traditionally used in species of this complex were examined to test the utility of each for species separation.

As a working hypothesis, which was suggested by examination of hundreds of adult and hatchling turtles from the Stoddard population, I provisionally recognized two variable species, *G. ouachitensis* and *G. pseudogeographica* (hypothesis 2, above). The number of complete and broken crescents for 514 *G. ouachitensis* and 423 *G. pseudogeographica* adults from Stoddard were tabulated (Table 2).

Table 2.—Number of lines entering the orbit in populations of *G. ouachitensis* and *G. pseudogeographica*; samples of both species on the same line are from sympatric populations (−1, complete postorbital crescent; 0, incomplete postorbital crescent, no lines entering orbit; +1 to +9, number of lines entering orbit).

State	<i>G. ouachitensis</i>				<i>G. pseudogeographica</i>			
	N	Mean	Range	SD	N	Mean	Range	SD
Wisconsin	514	0.76	−1–5	0.87	423	3.20	0–8	1.20
South Dakota	—	—	—	—	41	4.95	0–8	1.17
Illinois	36	2.47	−1–7	4.03	42	5.96	−1–7	3.43
Indiana	13	4.38	2–7	1.81	8	4.19	−1–7	2.53
Iowa	13	2.00	1–3	1.66	5	3.50	3–6	—
West Virginia	4	3.50	3–5	—	—	—	—	—
Kentucky	4	4.38	0–7	—	2	−1	—	—
Tennessee	25	3.62	−1–8	0.83	171	3.58	−1–8	2.54
Missouri	—	—	—	—	8	3.88	2–7	0.75
Arkansas	83	3.46	−1–6	1.30	136	0.02	−1–7	1.34
Kansas	10	3.05	1–4	0.87	1	6.00	—	—
Oklahoma	75	3.97	1–6	3.10	—	—	—	—
Texas	3	3.67	3–4	—	39	−0.54	−1–3	0.003
Louisiana	54	2.51	−1–6	1.68	314	−0.28	−1–6	0.58
Alabama	5	3.20	3–4	—	—	—	—	—
Louisiana, Sabine River	57	6.51	4–9	0.98	38	−1	−1	0
Mississippi	1	4.00	—	—	39	−0.19	−1–3	0.62
	899				1277			

The range of variation in the number of lines entering the orbit is so great in both species (*G. ouachitensis*: −1 to 5, \bar{x} = 0.76; *G. pseudogeographica*: 0 to 8, \bar{x} = 3.2) and the overlap so large, that this character alone could not be used to separate the species. Therefore, adults were assigned to species according to the size of postorbital, subocular, and throat spots (Fig. 1). Some females with intermediate-sized postorbital, subocular, and throat spots appeared to be intermediate between the two species, suggesting hybridization (Cagle, 1953). Hatchlings resulting from incubation (at 28°C) of eggs collected from these intermediate females, however, were all clearly *G. ouachitensis*, confirming the identity of the parents. Part of the variation in spot size in the Stoddard *G. ouachitensis* population apparently results from the different temperature regimes to which natural nests are subjected. Ewert (1979) incubated *G. ouachitensis* eggs from Indiana and the Mississippi River in Minnesota at 25°C and 30°C. He found that complete crescents (=larger spots) occurred predominately in *G. ouachitensis* incubated at 25°C; their siblings incubated at 30°C had very few crescents.

Inheritance and the influence of incubation temperature on head pattern variability. —Clutches of eggs from female *G. ouachitensis* and *G. pseudogeographica* from Stoddard, assigned to species on the basis of head pattern characters, were incubated in the laboratory at 28°C. The head patterns of the resulting 317 hatchlings were compared with those of the female parents. Female *G. ouachitensis* with large postorbital, subocular, and throat spots produced similarly marked offspring, but also individuals with wide crescents and others with one to three lines entering the orbit. Females with wide crescents also produced offspring of all three pattern types. Some hatchlings had one side of the head with a crescent and the other with a broken crescent. None of the *G. ouachitensis* hatchlings had spots as small as or smaller than those of the female parent. All of the parent female *G. ouachitensis* had the underside of the head patterned with four spots

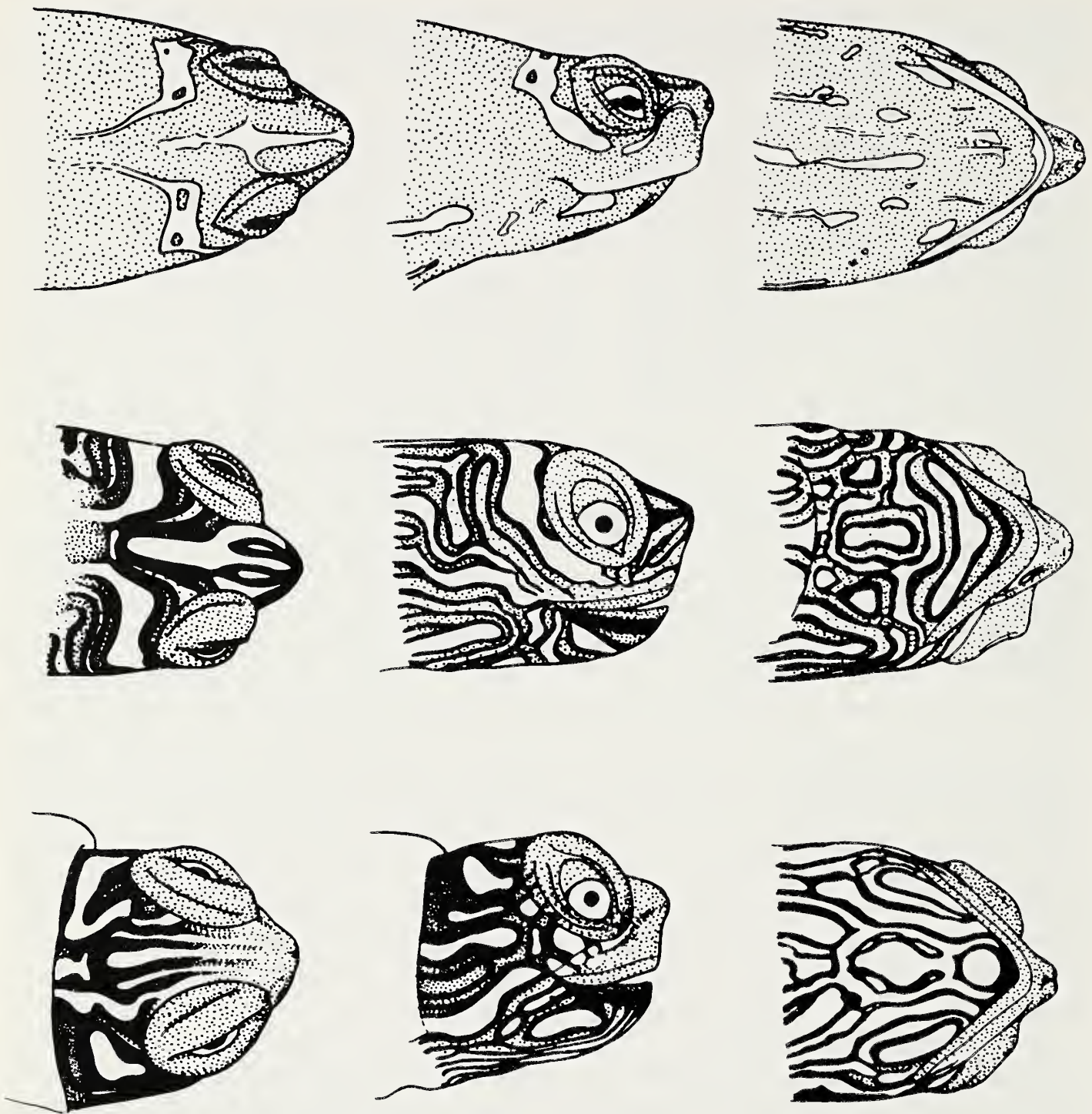


Fig. 3.—Head patterns of female *G. ouachitensis* from Stoddard, Vernon Co., Wisconsin (RCV 776, upper row) and offspring from eggs incubated at 25°C (UWZM 21658, middle row) and 35°C (UWZM 21655, lower row).

rather than crossbars. Four young, from three different clutches, had crossbars (Fig. 3).

All hatchlings of *G. pseudogeographica* had narrow postorbital spots, small subocular spots and small throat spots. No *G. pseudogeographica* females from Stoddard produced hatchlings with complete crescents. Only one hatchling had a postorbital marking that could be considered a partial crescent, which was similar to those found in Louisiana *G. pseudogeographica*.

To test the effect of various incubation temperatures on head markings, each of 11 clutches of *G. pseudogeographica* and 15 clutches of *G. ouachitensis* eggs was divided into three groups for incubation at 25°, 30°, and 35°C. The 30°C sample was lost due to equipment failure.

Only slight differences were noted between the patterns of hatchling *G. pseudogeographica* from 25°C and those of the 35°C group. No crescents were found in either group and more postorbital lines occurred in the 35°C group (3–6, \bar{x} = 4.8, N = 23) than in the 25°C group (3–5, \bar{x} = 3.9, N = 39). Complete wide crescents were found in six (15%) and broken crescents on three (7%) of *G. ouachitensis* hatchlings in the 25°C group, whereas none of the hatchlings in the 35°C group had crescents. Those incubated at 35°C averaged more postorbital lines on each side of the head (1–4, \bar{x} = 2.5, N = 25) than those at 25°C (–1–4, \bar{x} = 1.3, N = 46). In addition to the decrease in number of postorbital lines at 25°C, there was an increase in the size of the postorbital, subocular, mandibular, and chin spots, and widening of the sagittal stripe (Fig. 3). Ewert (1979) also noticed a temperature effect on sagittal stripe width.

Head marking areas of 46 *G. ouachitensis* and 39 *G. pseudogeographica* incubated at 25°C, and 12 *G. ouachitensis* and 8 *G. pseudogeographica* incubated at 35°C were compared through canonical analysis of raw data with dorsal head area used as a covariate. The first canonical variate separated *G. ouachitensis* from *G. pseudogeographica* and the second separated the effects of the two incubation temperatures (Fig. 4). Pairwise, Mahalanobis' distances between the four samples reach a maximum of 3.8 between *G. ouachitensis* incubated at 35°C and *G. pseudogeographica* at 25°C (Table 3). Separation of the two species was achieved primarily by contrast of the subocular spot area with the dorsal postorbital spot area, and chin spot area with the ventral mandibular spot area. Separation of the effects of incubation temperature was made on the basis of contrast of the ventral mandibular spot area with the subocular spot area, and ventral mandibular spot area with the dorsal postorbital spot area.

Thus much of the intrapopulation variation in head pattern in both *G. ouachitensis* and *G. pseudogeographica* can be attributed to the effect of incubation temperature. The basic pattern can be modified to the extent that *G. ouachitensis* incubated at high temperatures resemble *G. pseudogeographica*.

Geographic variation in head pattern.—A set of 100 head photographs was analyzed to test the feasibility of differentiating the forms of *Graptemys* by area and degree of roundness of specific head markings. The data were grouped into six populations: (1) 26 *G. ouachitensis* from Stoddard; (2) 24 *G. pseudogeographica* from Stoddard; (3) 20 *Graptemys* of intermediate pattern from Stoddard; (4) 10 *G. pseudogeographica* from DeVall's Bluff, Arkansas; (5) 10 *G. ouachitensis* from Illinois, Tennessee, and Oklahoma; and (6) 10 *G. pseudogeographica* from Reelfoot Lake, Tennessee. Individuals in groups 1 and 2 were chosen to represent the full range of variation in each species. Group 3 includes individuals difficult to place in either species on the basis of head pattern alone. Individuals in groups 4, 5, and 6 were chosen at random from specimens available. Canonical analysis of head pattern area is shown in Fig. 5. The first two canonical variates account for 89.4% of the variation in the six samples.

Separation of Wisconsin *G. pseudogeographica* and *G. ouachitensis* was primarily the result of contrasts between areas of the left subocular spot and dorsal left postorbital spot, chin spot and left mandibular spot, and right subocular spot and chin spot. The index of the degree of roundness of the head markings did not give a definitive separation between species or populations. Fig. 5 is a two-dimensional representation of the relationships of these populations.

Multiple discriminant analysis of head patterns separates Wisconsin *G. ouachitensis* and *G. pseudogeographica* (Table 4, Pop. 1 vs. Pop. 2), suggesting that at

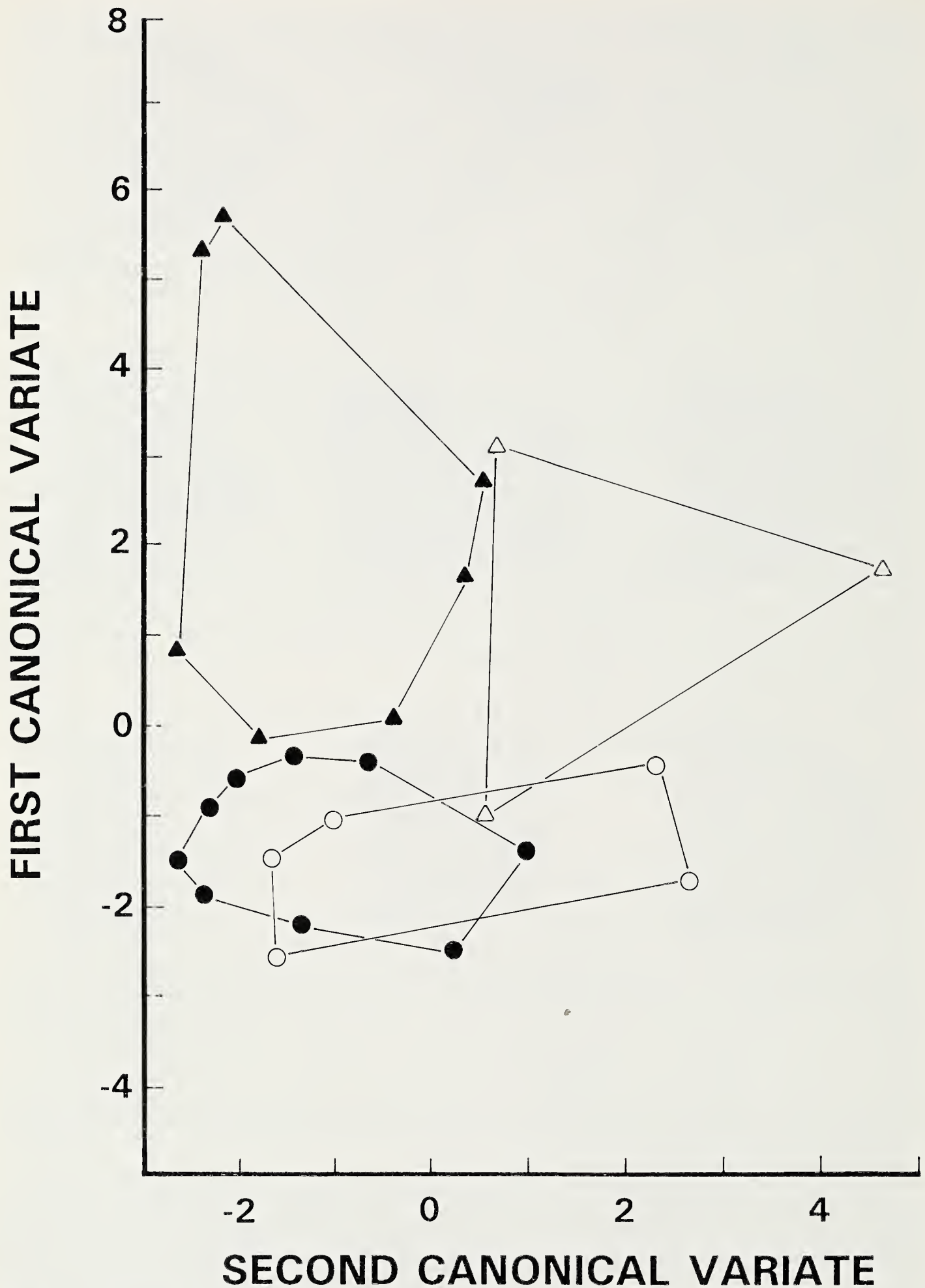


Fig. 4.—Canonical analysis of head pattern area (untransformed data, dorsal head area as covariate) of hatchling *G. ouachitensis* and *G. pseudogeographica* from Stoddard incubated at 25°C and 35°C. Symbols as follows: solid triangles, *G. ouachitensis* at 25°C; open triangles, *G. ouachitensis* at 35°C; solid circles, *G. pseudogeographica* at 25°C; open circles, *G. pseudogeographica* at 35°C. Variation in the first two canonical variates was 96.7% of variation in the four samples.

Table 3.—Pairwise Mahalanobis' distances (untransformed head pattern area, dorsal head area as covariate) between samples of hatchling *G. ouachitensis* and *G. pseudogeographica* from eggs incubated at 25°C and 35°C: Pop. 1, *G. ouachitensis* at 25°C; Pop. 2, *G. ouachitensis* at 35°C; Pop. 3, *G. pseudogeographica* at 25°C; Pop. 4, *G. pseudogeographica* at 35°C.

	Pop. 1	Pop. 2	Pop. 3	Pop. 4
Pop. 1	0.0			
Pop. 2	3.3	0.0		
Pop. 3	3.3	3.8	0.0	
Pop. 4	3.7	3.0	1.9	0.0

Stoddard *G. ouachitensis* and *G. pseudogeographica* are distinct species. However, the intermediacy of group 3 (Fig. 5) shows that head markings alone will not separate all individuals in the Stoddard population.

Skull Morphometrics

Skulls from Stoddard specimens of *G. ouachitensis* and *G. pseudogeographica* were qualitatively separable on the basis of flatness across the frontal, extension of the supraoccipital spine, and intersquamosal width. About 90% of skulls were consistently placed by me and an unbiased observer (E. Pilleart) into two groups. Measurements (Fig. 2) were chosen to quantify these qualitative differences in skull shape. Skull characters from 76 females were compared by canonical analysis using carapace length and width as covariates (Fig. 6). The first canonical variate primarily separated *G. ouachitensis* from *G. pseudogeographica*, whereas the second separated local populations of both species. The ratio of dentary width to carapace height and plastron width to pterygoid width were responsible for the separation of *G. ouachitensis* from *G. pseudogeographica* (Fig. 6). Intraspecific separations were made by the ratio of plastron width to dentary width. The Mahalanobis' distances (Table 5) show that the Wisconsin *G. pseudogeographica* population is closer to the southern *G. pseudogeographica* population than the Wisconsin *G. ouachitensis* population is to southern *G. ouachitensis*. The ratio of dentary width to pterygoid width separated Wisconsin *G. ouachitensis* from Wisconsin *G. pseudogeographica* by a distance of 4.36 standard deviations, when either carapace length or carapace width were used as covariates.

Canonical analysis of head pattern data combined with skeletal data for the Stoddard populations of the two species (Pop. 1 and Pop. 2) gave a separation of 11.03 standard deviations (Fig. 7). The ratios of carapace width to right mandible

Table 4.—Pairwise Mahalanobis' distances (untransformed head pattern area, dorsal head area as covariate) between six populations of *G. ouachitensis* and *G. pseudogeographica*: Pop. 1, Wisconsin *G. ouachitensis*; Pop. 2, Wisconsin *G. pseudogeographica*; Pop. 3, Wisconsin intermediates; Pop. 4, Arkansas *G. pseudogeographica*; Pop. 5, southern *G. ouachitensis*; Pop. 6, southern *G. pseudogeographica*.

	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5	Pop. 6
Pop. 1	0.0					
Pop. 2	4.7	0.0				
Pop. 3	3.2	2.8	0.0			
Pop. 4	5.1	4.2	3.1	0.0		
Pop. 5	3.1	4.0	1.5	3.4	0.0	
Pop. 6	3.9	3.0	1.0	2.6	2.0	0.0

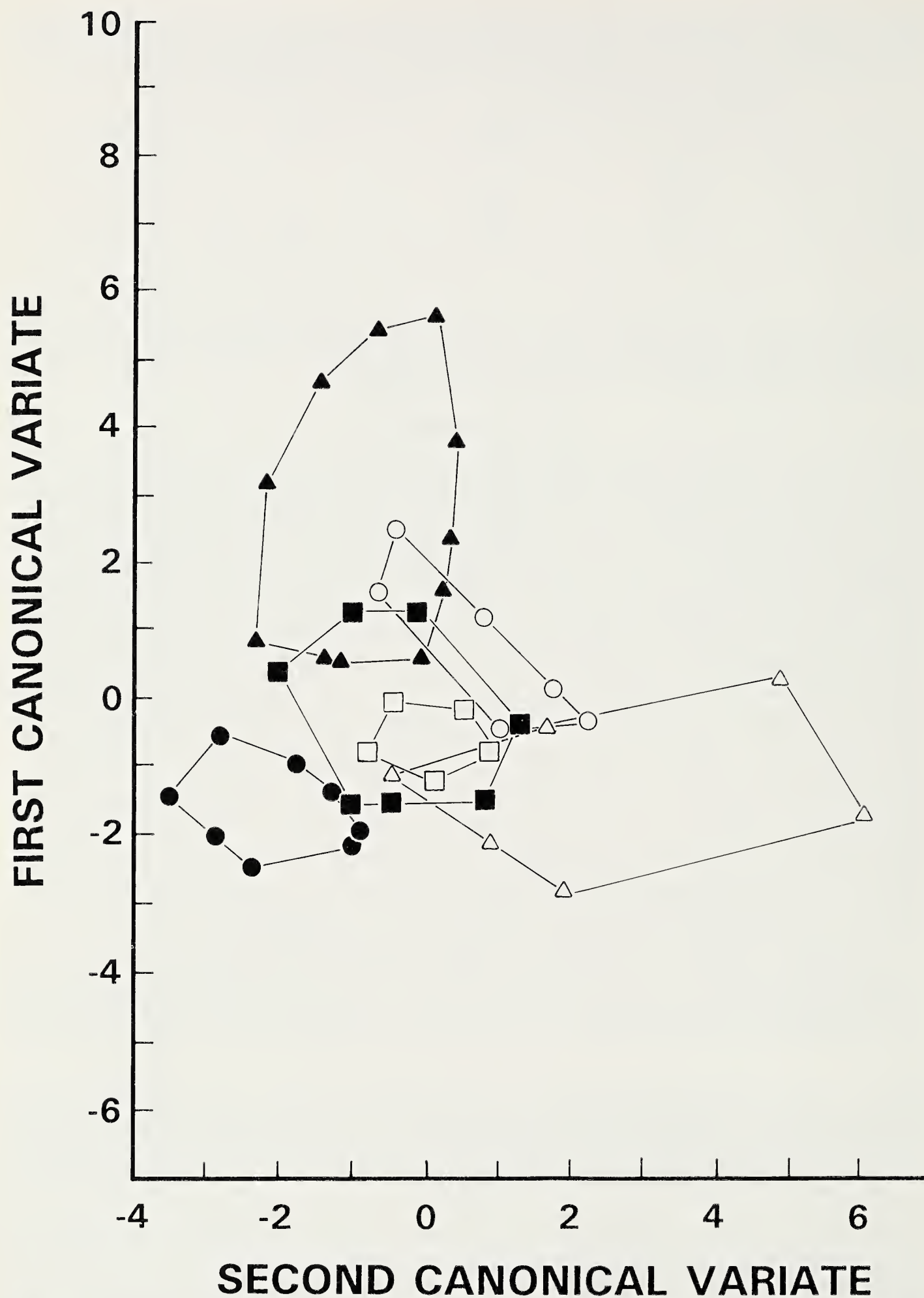


Fig. 5.—Canonical analysis of head pattern area (untransformed data, dorsal head area as covariate) of six populations of *G. ouachitensis* and *G. pseudogeographica*. Symbols as follows: solid triangles, Wisconsin *G. ouachitensis*; solid circles, Wisconsin *G. pseudogeographica*; solid squares, Wisconsin intermediates; open circles, southern *G. ouachitensis*; open triangles, Arkansas *G. pseudogeographica*; open squares, southern *G. pseudogeographica*.

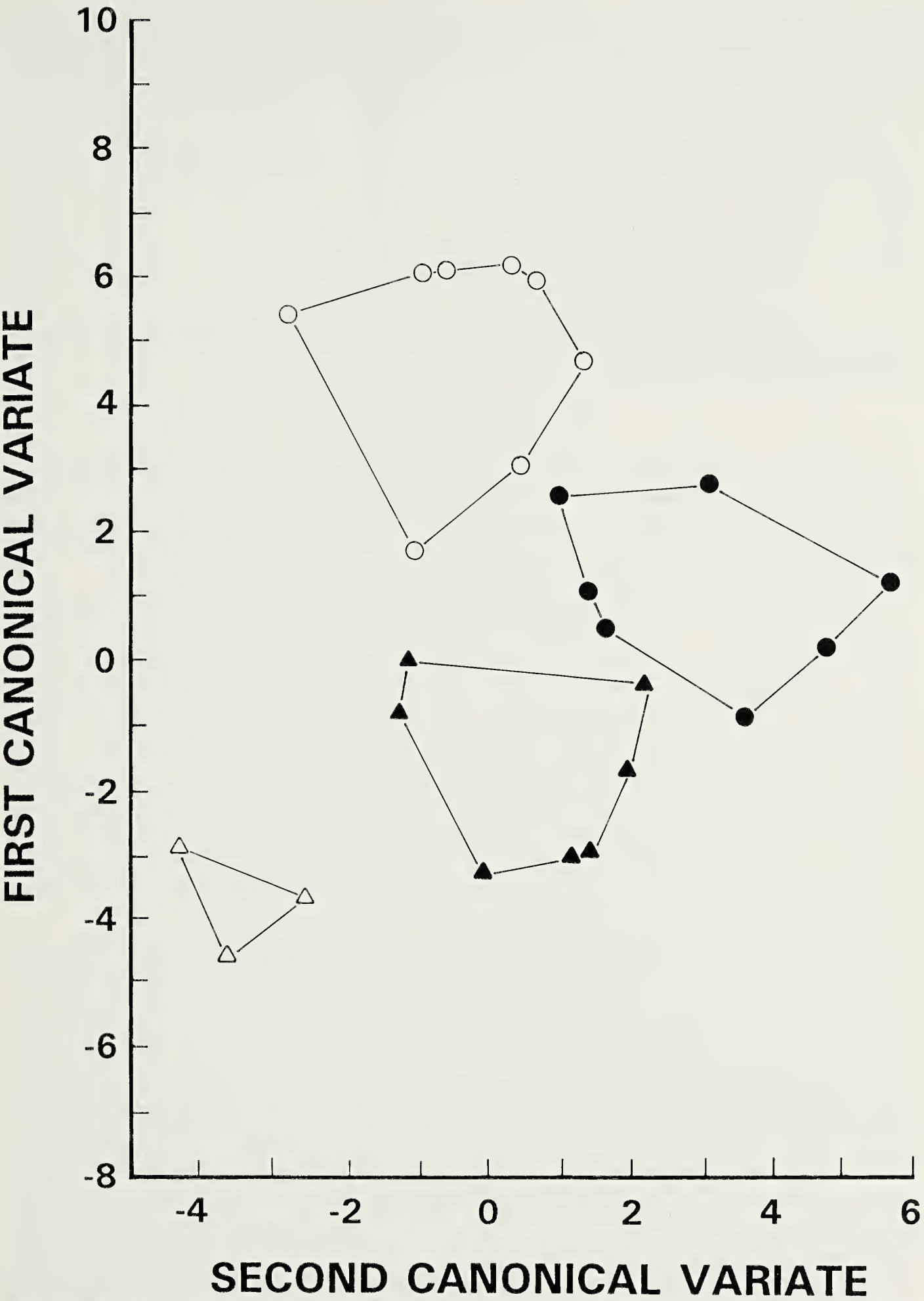


Fig. 6.—Canonical analysis of 15 skull characters, carapace height, plastron length and width (log transformed data, carapace length and width as covariates) of females from four populations of *G. ouachitensis* and *G. pseudogeographica*. Symbols as follows: solid circles, Wisconsin *G. pseudogeographica*; solid triangles, Wisconsin *G. ouachitensis*; open circles, Arkansas *G. pseudogeographica*; open triangles, Oklahoma *G. ouachitensis*.

Table 5.—Pairwise Mahalanobis' distances (log transformed skull measurements, carapace height, plastron length and width, carapace length and width as covariates) between samples of females from four populations of *G. ouachitensis* and *G. pseudogeographica*: Pop. 1, Wisconsin *G. pseudogeographica*; Pop. 2, Wisconsin *G. ouachitensis*; Pop. 3, Arkansas *G. pseudogeographica kohni*; Pop. 4, Oklahoma *G. ouachitensis*.

	Pop. 1	Pop. 2	Pop. 3	Pop. 4
Pop. 1	0.0			
Pop. 2	3.9	0.0		
Pop. 3	5.2	6.6	0.0	
Pop. 4	8.3	5.4	9.3	0.0

spot area and, secondarily, of plastron width to maximum skull width were responsible for the separation.

Shell Pattern

Variation in adult shell pattern.—The color patterns of carapace and plastron were analyzed in samples of *G. ouachitensis* and *G. pseudogeographica* from throughout their geographic ranges. The intraspecific diversity of carapace and plastron patterns in a large sample from a single population (Stoddard), and variation throughout the range of each species are shown in Table 6.

The carapace is usually light green or brown in ground color, and is marked with darker brown or black blotches. Each blotch may be ringed with an orange-yellow or light green line. The rings may interconnect to form a lattice across the entire carapace, with or without black blotches present. Some individuals have concentric rings. Usually there is only one black blotch at the posterior edge of each scute, but some individuals have more than one blotch per scute. The presence of a lattice of interconnecting rings is much more common in Wisconsin *G. pseudogeographica* than in Wisconsin *G. ouachitensis*, particularly in hatchlings. A major difference between adult Wisconsin *G. ouachitensis* and *G. pseudogeographica* is the frequency of occurrence of melanism. In the Stoddard sample, 16.3% of female and 5.5% of male *G. ouachitensis* were melanistic. No melanistic *G. pseudogeographica* were found.

Among the nine categories of plastral patterns (Table 6) there are consistent differences in frequency of occurrence between the species at Stoddard, and between adult males and adult females of each species. The plastron of hatchlings of both species is marked with interconnecting swirls of dark green to black on a yellow or cream ground color (Fig. 8). The amount of the plastron that is covered with these markings varies in both species, but *G. pseudogeographica* has a greater portion of the plastron covered by markings than does *G. ouachitensis*. Less than half of the *G. ouachitensis* hatchlings had 75% of the plastron covered by swirls while nearly all (94.4%) of the *G. pseudogeographica* had at least 75% of the plastron covered. Reduction of the dark green or black swirls to dark lines along the sutures occurred in 20.5% of *G. ouachitensis* hatchlings, but only in 0.5% of *G. pseudogeographica* hatchlings.

Males of both species retain the hatchling plastral pattern after maturity, thus the interspecific differences noted in hatchlings are also found in adult males. Adult females of *G. pseudogeographica* and *G. ouachitensis* differ very little in plastral pattern. Most have a mottled yellow-brown plastron without pattern,

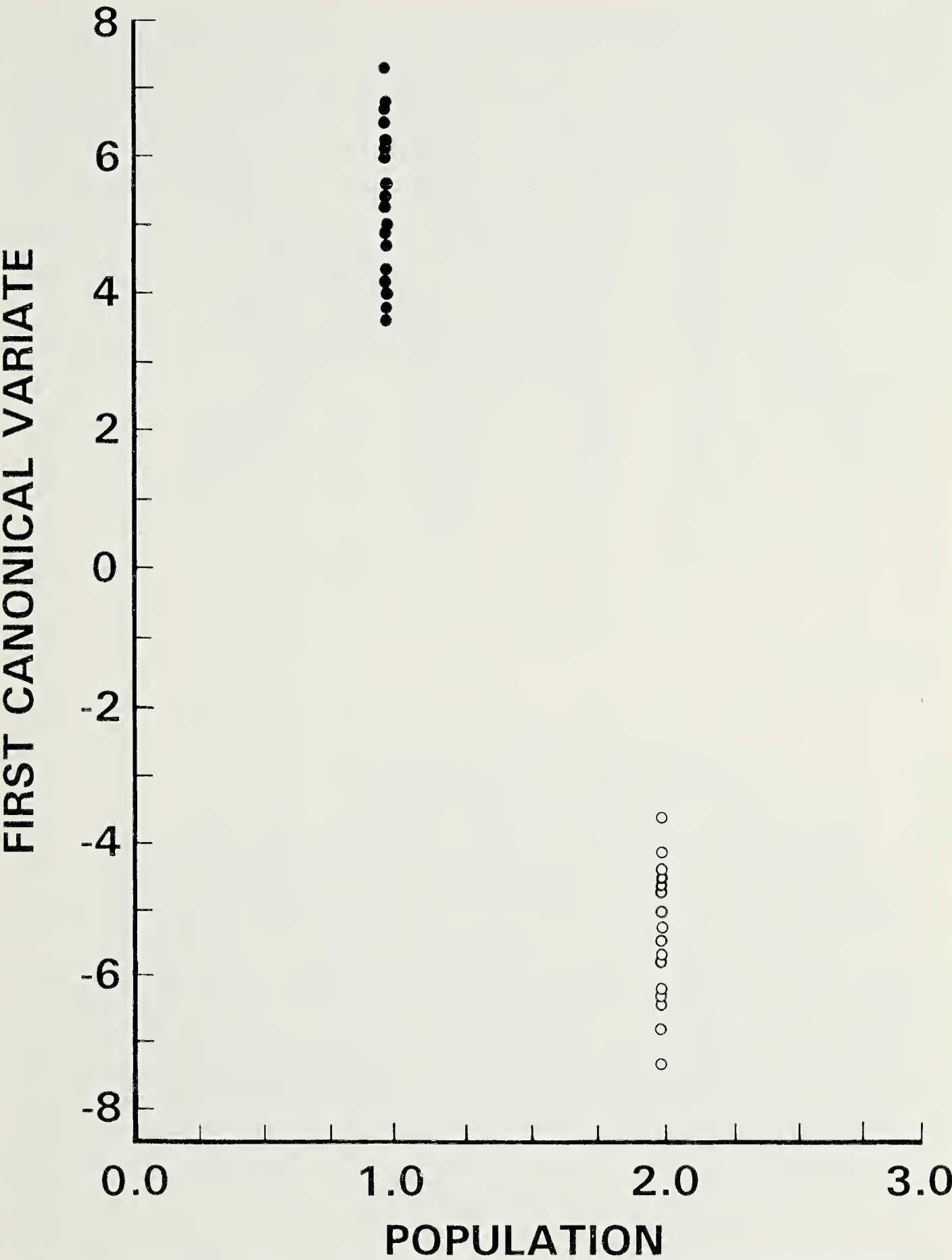


Fig. 7.—Canonical analysis of all head pattern, skull, and shell measurement characters (untransformed data, dorsal head area and carapace length as covariates) of female *G. ouachitensis* (open circles) and *G. pseudogeographica* (solid circles) from Wisconsin.

Table 6.—Frequency distributions of shell pattern characters in *G. ouachitensis* (*G. o.*) and *G. pseudogeographica* (*G. p.*) populations. Population codes are as follows: 1, Wisconsin *G. p.* females (*N* = 200); 2, Wisconsin *G. p.* males (*N* = 37); 3, non-Wisconsin *G. p.* both sexes (*N* = 211); 4, all *G. p.* (*N* = 448); 5, Wisconsin *G. o.* females (*N* = 200); 6, Wisconsin *G. o.* males (*N* = 55); 7, non-Wisconsin *G. o.* both sexes (*N* = 200); 8, all *G. o.* (*N* = 455); 9, *G. o. sabinensis* both sexes (*N* = 56); 10, Wisconsin *G. p.* hatchlings (*N* = 207); 11, Wisconsin *G. o.* hatchlings (*N* = 110). Pattern codes are as follows: Carapace: A, black blotch with orange, yellow, or light-green ring; B, same but ring faint; C, black blotch, no orange lines; D, no black blotch, rings connected by orange or yellow lattice; E, black blotch, rings, and lattice present; F, more than one black blotch per scute; G, concentric light rings with or without light centers; H, yellow or orange reticulation; I, melanistic; J, no markings (faded). Plastron: A, pattern distinct, covers >90%; B, pattern distinct, covers >75%; C, pattern distinct, covers >50%; D, pattern distinct along sutures; E, pattern outlined in black; F, yellow-brown mottled; G, yellow, unmarked; H, melanistic; I, concentric dark central figure.

	1	2	3	4	5	6	7	8	9	10	11
Carapace patterns											
A	18.0	43.2	22.5	21.9	13.9	34.6	46.0	30.3	39.3	39.1	51.0
B	34.0	13.5	38.5	34.6	34.7	41.8	23.7	30.8	10.7	0	0
C	34.0	5.4	5.6	18.3	24.8	9.1	3.0	13.4	0	0.5	4.5
D	0	16.2	6.6	4.5	1.5	1.8	9.6	5.1	1.8	48.3	14.5
E	4.0	13.5	8.9	6.5	0	3.6	5.1	2.6	3.6	0	0
F	10.0	8.1	2.8	7.1	8.9	3.6	2.5	5.5	3.6	3.4	13.6
G	0	0	0.5	0.2	0	0	3.0	1.3	41.1	7.7	15.5
H	0	0	0	0	0	0	5.1	2.2	0	0	0.9
I	0	0	1.9	0.9	16.3	5.5	2.0	8.8	0	0	0
J	0	0	12.7	6.0	0	0	0	0	0	0	0
Plastral patterns											
A	8.2	56.4	11.3	13.8	0	3.5	16.9	7.9	12.5	73.0	10.8
B	0	7.7	16.4	8.5	0	15.5	23.9	12.5	48.2	21.4	37.4
C	0	0	11.3	5.4	0	12.1	13.4	7.0	7.1	5.1	31.3
D	0	0	9.5	4.3	0	8.7	12.0	6.3	3.6	0.5	20.5
E	4.1	25.6	3.3	5.6	9.6	31.0	2.5	8.7	7.1	0	0
F	77.6	7.7	38.0	52.7	81.4	24.1	17.4	50.9	3.6	0	0
G	4.1	0	8.5	5.8	1.7	0	6.0	3.3	0	0	0
H	6.1	2.6	0	2.9	7.3	5.2	0	0	0	0	0
I	0	0	1.9	0.9	0	0	8.0	3.5	17.8	0	0

although some individuals of both species retain a black outline of the hatchling pattern.

Ontogenetic changes in shell pattern.—Shell patterns of 207 *G. pseudogeographica* and 110 *G. ouachitensis* hatchlings from Stoddard were photographed and categorized according to the patterns listed in Table 6 in December 1972, four months after hatching. Each year for the next five years shell patterns were recorded for each individual so that changes in pattern could be followed. Like the head pattern, the plastral pattern is unique in each individual, and can be used for individual identification during the first two years in females, and for at least five years in males. During the second year the plastral pattern of females fades and dark pigment begins to fill the light spaces; the entire plastral pattern is usually obliterated by the end of the third year. During the second year dark pigment begins to concentrate at the posterior edges of the plastral scutes forming dark lines along the seams. This differs from the hatchling pattern in which dark pigment is distributed on both sides of the seams. Although the hatchling plastral pattern remains distinct in most males throughout life, many of the finer lines, useful for individual identification, fade.

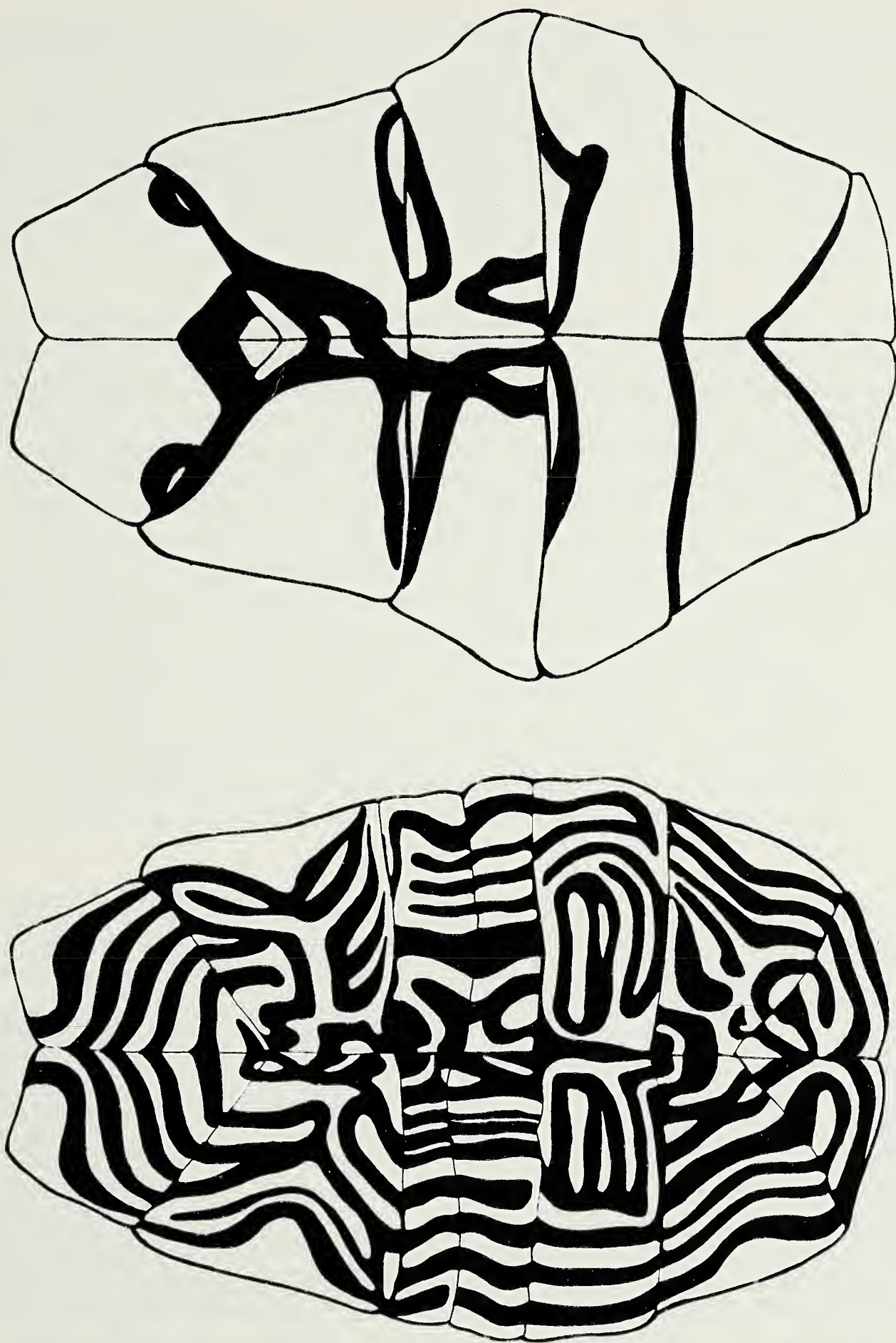


Fig. 8.—Plastral patterns of hatchling *G. ouachitensis* (top) and *G. pseudogeographica* (bottom) from Stoddard, Wisconsin.

Table 7.—Species, localities, and sample sizes of populations examined by electrophoresis.

Species	N	Locality
<i>G. p. pseudogeographica</i>	85	Wisconsin, Vernon Co., Stoddard, Mississippi River
<i>G. p. kohni</i>	25	Arkansas, Prairie Co., DeVall's Bluff, White River
<i>G. o. ouachitensis</i>	96	Wisconsin, Vernon Co., Stoddard, Mississippi River
<i>G. o. ouachitensis</i>	18	Arkansas, Prairie Co., DeVall's Bluff, White River
<i>G. o. sabinensis</i>	14	Louisiana, Sabine River
	238	

The carapace pattern of hatchlings differs in several ways from that of adults in both *G. pseudogeographica* and *G. ouachitensis*: hatchlings have gray or light brown ground color rather than green; the areas in the centers of the orange rings are often bright orange or yellow rather than black; the orange or yellow lines are much more distinct; and the marginal scutes are often marked with three parallel longitudinal orange bars or an orange ring with an orange bar in the center of it.

In both species, the orange rings become less distinct with age. The black blotches in the centers of the orange rings become more distinct in the first 3½ years of growth. Individuals which had an orange lattice without black blotches developed black blotches in the centers of the rings within 2½ years. The pattern in five *G. pseudogeographica* changed from orange rings with black centers to orange rings without black spots in three years. In 3½ years two *G. pseudogeographica* that had an orange lattice lost all trace of pattern. By the end of five years of growth, the carapace pattern in *G. pseudogeographica* was not noticeably different from that at three years. In *G. ouachitensis* hatchlings, patterns went from orange reticulations or lattice to orange rings with black blotches in two years, and six females became entirely melanistic in three years. As in *G. pseudogeographica*, the pattern stabilized after five years.

Electrophoresis

Comparisons were made of the electrophoretic mobilities of 19 protein systems in 110 *G. pseudogeographica* and 128 *G. ouachitensis* from Wisconsin, Arkansas, and Louisiana (Table 7). No differences were found between males and females, or between fresh and frozen material. Identical mobilities were displayed at the LDH-1, LDH-2, LDH-3, MDH-1, MDH-2, and GOT-2 loci for all individuals examined. Many protein systems did not show distinct bands, probably due to polymerization (McKown, 1972); they were compared by measuring the greatest distance migrated. Insignificant relative migration differences (0.01–0.03) were found at the H-EST, H-ESS, H-GEN, H-PEP-1, H-PEP-2, H-PEP-3, LAP, P-GP, PPEP-1, and M-GP loci.

Small, but consistent mobility differences (Table 8) were found between species at the plasma esterase (P-EST) locus (Fig. 9). Plasma peptidase-2 (PPEP-2) also varied in mobility between populations and between species, but the differences (0.02–0.05) were neither sufficiently great nor consistent to determine population differences.

The MDH-3 locus was the only heterozygous locus found among the 19 loci studied. Variation was present between species and between subspecies, within populations, within clutches, and between offspring and parent. The MDH-1 and MDH-2 bands were consistently light, but identical for all individuals examined. Both species were found to possess three different alleles for MDH-3, represented

Table 8.—Relative mobility comparisons between populations for plasma esterase (P-EST).

Populations	Mobility difference
Wisconsin, <i>G. ouachitensis</i> : Arkansas, <i>G. ouachitensis</i>	0.08
Wisconsin, <i>G. pseudogeographica</i> : Arkansas, <i>G. pseudogeographica</i>	0.03
Arkansas, <i>G. ouachitensis</i> : Arkansas, <i>G. pseudogeographica</i>	0.06
Wisconsin, <i>G. ouachitensis</i> : Wisconsin, <i>G. pseudogeographica</i>	0.08
Arkansas, <i>G. ouachitensis</i> : Louisiana, <i>G. ouachitensis sabinensis</i>	0.00

by the third (cc), fourth (aa), and fifth (abc) individuals in Fig. 10. This gel compares three clutches of *G. ouachitensis* hatchlings with three clutches of *G. pseudogeographica* hatchlings from Wisconsin. The first, 12th, and 26th positions are *Chrysemys picta belli*; the other positions alternate between *G. ouachitensis* and *G. pseudogeographica*, beginning with *G. ouachitensis* in the second position.

Table 9 compares the occurrence of MDH-3 allozymes in clutches of hatchlings, and in hatchlings and their female parent. The allozymes present in *G. ouachitensis* females L1, L2, and L3 were all different from those present in their offspring. Clutch L1 included individuals with two different allozymes, both different from the female parent. Intra-clutch variation was also noted in two other *G. ouachitensis* clutches, and in four *G. pseudogeographica* clutches. Table 10 summarizes frequencies of the three allozymes in pooled samples. The cc phenotype occurred in 78% of *G. pseudogeographica* hatchlings, but only in 29% of *G. ouachitensis* hatchlings. The abc phenotype was more common in *G. ouachitensis* hatchlings (59%) than in *G. pseudogeographica* hatchlings (20%). The aa phenotype was rare in both species: 2% in *G. pseudogeographica* and 10% in *G. ouachitensis*. *Graptemys ouachitensis* adults, like the hatchlings, had a greater percentage of indi-

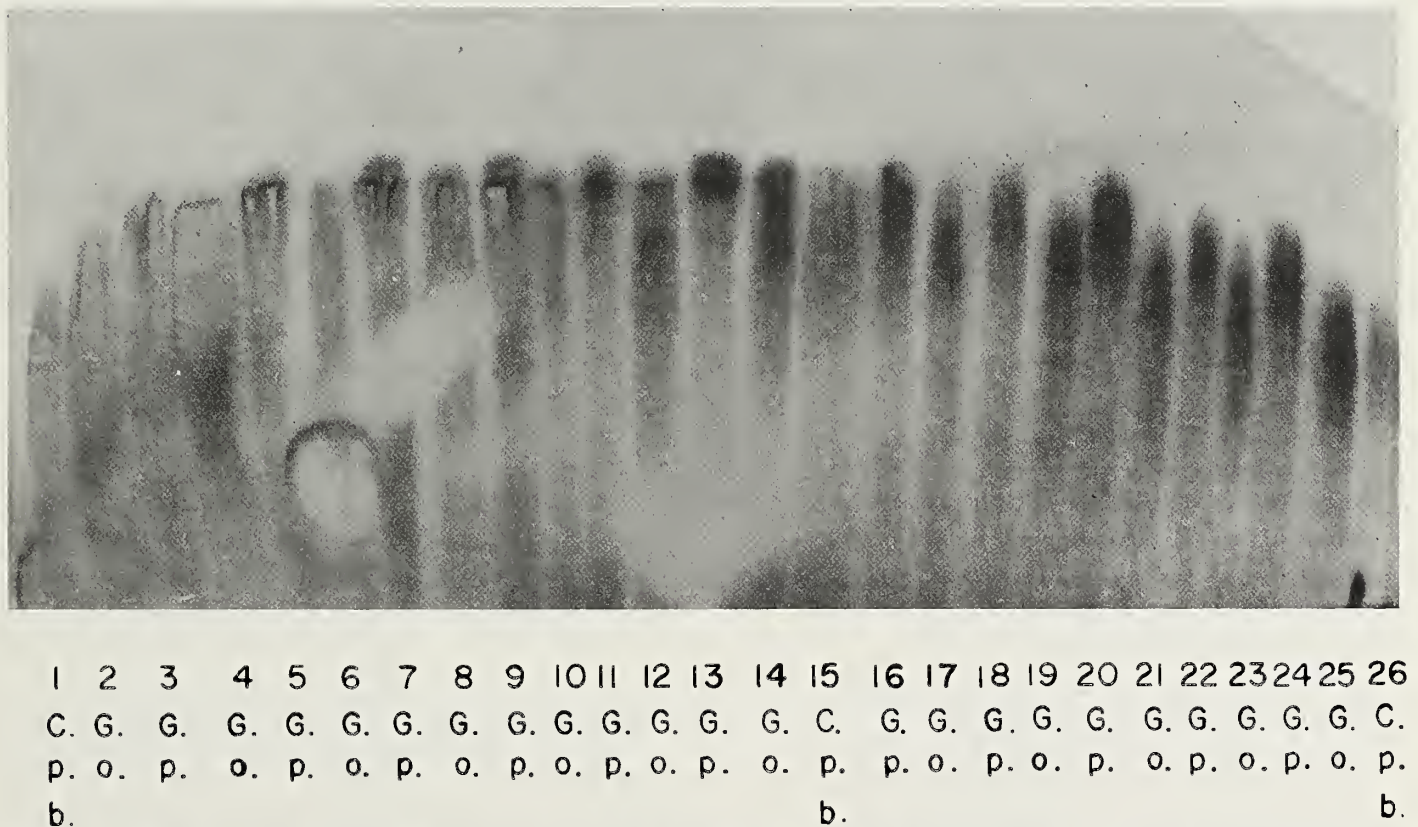
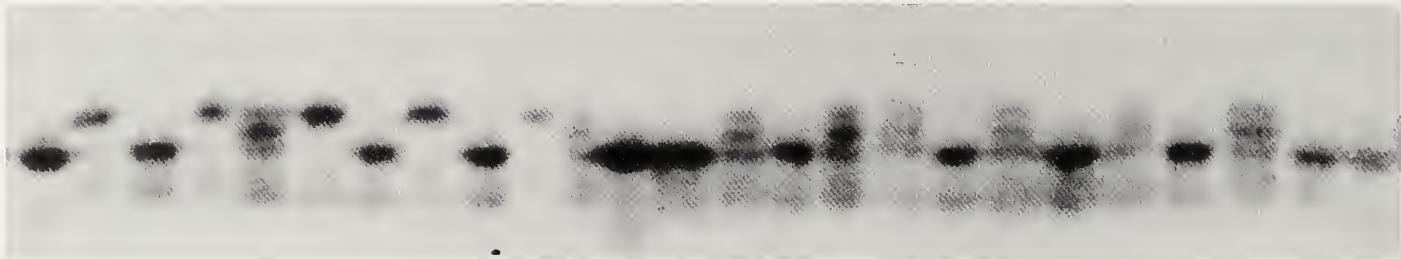


Fig. 9.—Electropherogram of plasma esterase (P-EST) in whole clutches of *G. pseudogeographica* (*G. p.*) and *G. ouachitensis* (*G. o.*) from Stoddard, Wisconsin. *C. p. b.*, *Chrysemys picta belli*.



1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
C. G. G. G. G. G. G. G. G. G. C. G. G. G. G. G. G. G. G. G. G. C.
p. o. o. o. o. o. o. o. o. o. p. o. o. o. o. o. o. o. o. o. o. p.
b. o. b. b.

Fig. 10.—Electropherogram of malate dehydrogenase (MDH-3) in whole clutches of *G. pseudogeographica* (*G. p.*) and *G. ouachitensis* (*G. o.*) from Stoddard, Wisconsin. *C. p. b.*, *Chrysemys picta belli*.

viduals carrying the abc phenotype than did the *G. pseudogeographica* adults in all of the populations sampled. Most (82%) of the *G. pseudogeographica* were of the cc phenotype compared to only 48% of the *G. ouachitensis*.

Courtship Behavior

Courtship behavior of *G. ouachitensis* and *G. pseudogeographica* from Stoddard was observed in the laboratory. Courtship behavior in both species is similar to that observed by Jackson and Davis (1972) for *Pseudemys*. Titillation has been reported for *G. pseudogeographica* (Cagle, 1955; Ernst, 1974), but no attempt has been made to quantify the behavioral patterns associated with courtship.

Presentation experiments were conducted with a male of one species in a 20-gallon aquarium behind one-way glass. After the male had been habituated 2 hr, one female of each species was placed in the tank with the male. The phases of courtship behavior are remarkably similar in both *G. pseudogeographica* and *G. ouachitensis* (Fig. 11). When the male observed a conspecific female, he would either raise his head and swim to a nose to nose position with the female and initiate courtship, or place his nostrils in the proximity of the female's cloaca. If the latter occurred he would then attempt to mount, trail behind the female with neck outstretched, or assume a nose to nose posture and initiate courtship.

Table 9.—Occurrence of MDH-3 allelomorphs in *G. ouachitensis* and *G. pseudogeographica* clutches.

Population	Allelomorph		
	cc	aa	abc
<i>G. ouachitensis</i> Clutch L ₁ + ♀	2	♀	3
<i>G. ouachitensis</i> Clutch L ₂ + ♀	♀	2	0
<i>G. ouachitensis</i> Clutch L ₃ + ♀	0	3	♀
<i>G. ouachitensis</i> wild hatched clutch	7	0	2
<i>G. ouachitensis</i> hatchlings of 653	0	0	1.3
<i>G. ouachitensis</i> hatchlings of 76-5	3	0	6
<i>G. pseudogeographica</i> hatchlings of 76-1	6	0	3
<i>G. pseudogeographica</i> hatchlings of 76-3	11	0	4
<i>G. pseudogeographica</i> hatchlings of 76-4	5	0	0
<i>G. pseudogeographica</i> hatchlings of 418	3	0	3
<i>G. pseudogeographica</i> hatchlings of 651	4	0	0
<i>G. pseudogeographica</i> hatchlings of 659	7	0	0
<i>G. pseudogeographica</i> hatchlings of 663	4	1	0

Table 10.—Summary of frequency of occurrence of MDH-3 allelomorphs (percentages) in sampled populations of *G. ouachitensis* and *G. pseudogeographica*.

Population	Allelomorph			N
	cc	aa	abc	
<i>G. pseudogeographica</i> all hatchlings	78	2	20	51
<i>G. ouachitensis</i> all hatchlings	29	12	59	41
<i>G. pseudogeographica</i> Wisconsin adults	78	3	19	34
<i>G. ouachitensis</i> Wisconsin adults	44	8	48	55
<i>G. ouachitensis</i> Arkansas adults	72	0	28	18
<i>G. pseudogeographica</i> Arkansas adults	88	0	12	25
<i>G. o. sabinensis</i> Louisiana	64	14	22	14
Total <i>G. pseudogeographica</i>	82	2	16	110
Total <i>G. ouachitensis</i>	48	10	42	128

In the nose to nose posture the male rotated the forearms toward the medial plane and drummed the backs of the foreclaws against the ocular region of the female (“titillation”). The duration of titillation bouts in milliseconds (msec) was similar in the two species (*G. ouachitensis* \bar{x} = 454 ± 126 (281–750), N = 23; *G. pseudogeographica* \bar{x} = 468 ± 142 (344–843), N = 24). But the number of strokes per bout in *G. pseudogeographica* is about twice that of *G. ouachitensis* (*G. p.*, \bar{x} = 10.3 ± 2.3 (7–14), N = 24; *G. o.*, \bar{x} = 5.2 ± 1.28 (4–8), N = 23).

High speed motion pictures of turtles taken from the lateral aspect revealed additional species-specific differences. During the initiation of foreclaw drumming, the head of male *G. pseudogeographica* is bobbed in the vertical plane, and that of *G. ouachitensis* is held stationary. On four occasions the mouth was opened and closed in rapid succession while a male *G. pseudogeographica* was performing

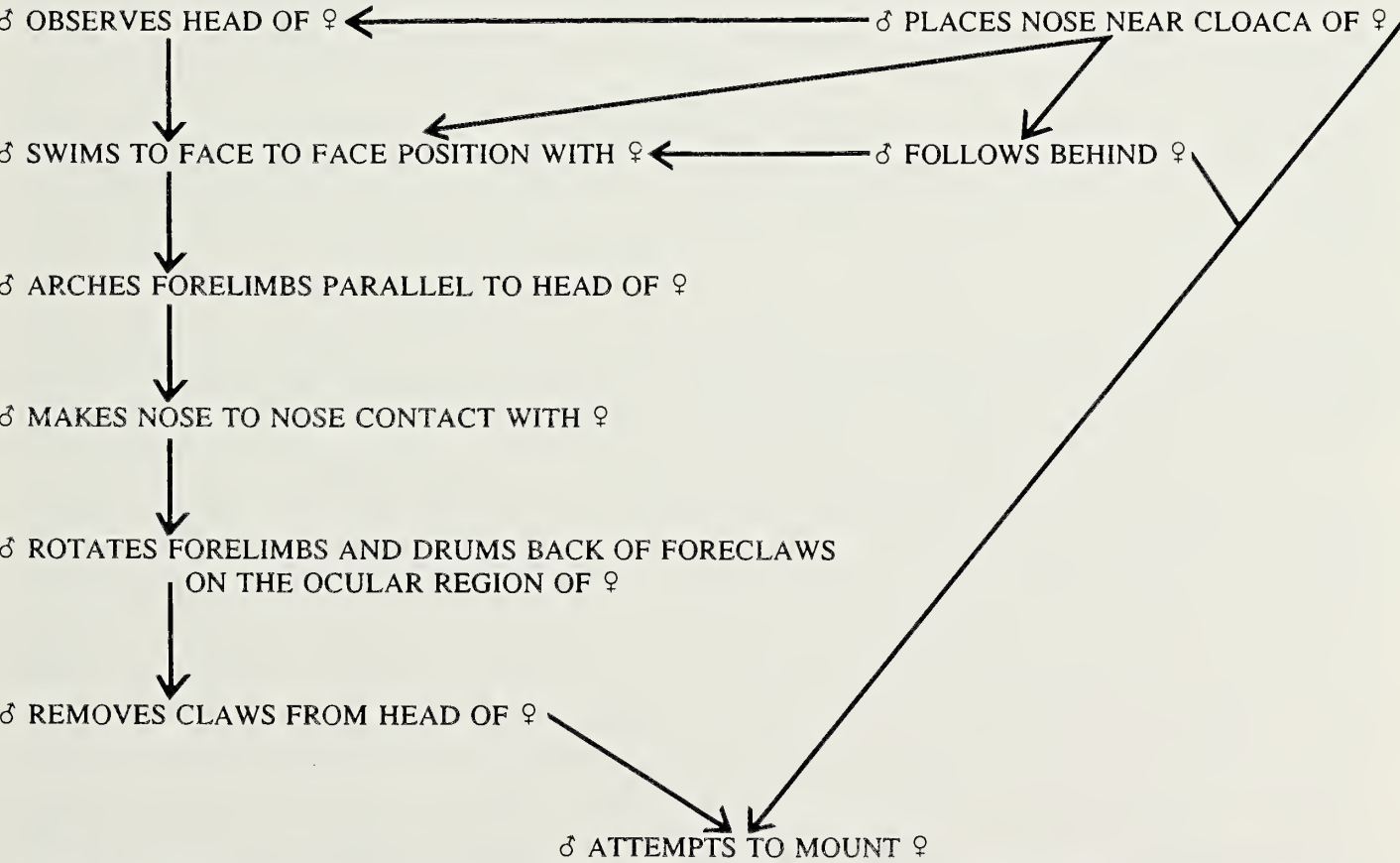


Fig. 11.—Generalized courtship sequence of male *G. ouachitensis* and *G. pseudogeographica*.

a titillation bout. Analysis of 15 bobbing sequences of *G. pseudogeographica* males showed two different patterns, either up-down-up-down-up or up-down-up. The sequence was always terminated by an upward bob. The duration of a single bob (up or down) averaged 78.1 msec. Each bobbing sequence lasted from 219–406 msec ($N = 15$); with a mean of 392 msec ($N = 11$) when five bobs were made and 230 msec ($N = 4$) when three bobs were made.

GEOGRAPHIC VARIATION IN THE *GRAPTEMYS PSEUDOGEOGRAPHICA* COMPLEX

Head pattern.—Specimens from throughout the geographic ranges of *G. pseudogeographica* and *G. ouachitensis* were assigned to species on the basis of the head pattern characters noted above. Each specimen was given a value related to the presence of a crescent or broken crescent, or the number of lines entering the orbit (*see* Methods). Individuals of each species were then combined into groups by state or river system (Table 1). The mean head pattern value for each group was then calculated (Table 2). The range of values throughout the geographic range of each species is nearly the same, -1 to 8 for *G. pseudogeographica* and -1 to 9 for *G. ouachitensis*.

Clinal variation in the number of lines entering the orbit occurs along a north-south gradient in both species. *Graptemys ouachitensis* has the lowest value in Wisconsin and the highest in the Sabine River, whereas *G. pseudogeographica* has a high number of lines in the northern states (South Dakota and Illinois) compared to Louisiana and Texas (Table 2).

In *G. pseudogeographica* the postorbital crescent character shows a large area of heterogeneity in Louisiana, Arkansas, Tennessee, and southern Illinois. However, the homogeneity of populations with broken crescents in Wisconsin, Iowa, South Dakota, and Nebraska, and complete crescents in Oklahoma, Texas, and Louisiana supports maintenance of subspecies designations for populations at the extremes of the geographical range. The complete intergradation of head patterns between southern and northern populations of *G. pseudogeographica* (Table 2) verifies their conspecificity.

Complete crescents occur much less frequently in *G. ouachitensis*. The Wisconsin population has a higher percentage of crescents than any other (mean of less than one line entering the orbit, Table 2). If head patterns are important in species recognition (as courtship behavior suggests) the greatest difference in head pattern between species should occur in areas of sympatry. Examination of sympatric populations from which an adequate sample of both species was available reveals that the modal numbers of lines entering the orbit are dramatically different between the species in areas of sympatry (Table 11).

The maximum diameter of each head spot of 478 turtles from nine populations of *G. ouachitensis* and nine populations of *G. pseudogeographica* (Table 1 except for Pop. 15) were compared by canonical analysis. This character separated Sabine River *G. ouachitensis sabinensis* from the remaining populations due to the small postorbital spots and presence of transverse chin bars. The barred chin pattern is extremely different from the pattern in other populations which have three spots. It appears that these chin bars are formed by fusion of the spots. These characters separated this population at a minimum of 5.5 standard deviations.

Head marking areas of 265 *G. ouachitensis* from nine localities were used to compare variability within a species. The Wisconsin population was divided into three groups (male, female, and young) to examine the effects of age and sex.

Table 11.—Modal number of temporal lines entering the orbit in sympatric populations of *G. ouachitensis* and *G. pseudogeographica*.

	<i>G. ouachitensis</i>	<i>G. pseudogeographica</i>
Wisconsin	1	3
Illinois	2	5
Arkansas	3	−1
Tennessee	3	1
Louisiana	3	−1
Louisiana, Sabine River	5	−1

Distances between the three divisions of the Wisconsin population are not so great as to confound the analysis. On the contrary, the multiple discriminant analysis emphasized the diversity present in a large population. The lack of discrete separation of populations from Wisconsin, Illinois, Arkansas, Oklahoma, and Catahoula Parish, Louisiana, and other Louisiana populations indicated relatedness. Combining male, female, and young from the Wisconsin populations produced little change in the results. The Wisconsin population still grouped with Arkansas, Catahoula Parish, Oklahoma, and Illinois populations, with Tennessee, Indiana, West Virginia, and Sabine River populations on the periphery. The size of the head spots is the most important character separating populations. It separated *G. ouachitensis* from Indiana, West Virginia, and Tennessee from the others. The contrast between chin spot and postorbital spot areas placed the Sabine River population and the West Virginia population at opposite extremes, and separated them partially from the rest of the group. Over 75% of the Sabine River population clustered away from the rest of the specimens examined because of its small postorbital spots and narrow transverse chin bars. The Indiana and West Virginia specimens have much larger postorbital spots and chin spots in proportion to the head area than do other populations (Table 12).

Analysis of *G. pseudogeographica* samples showed a continuum of variation between northern and southern populations. Contrasts of the number of temporal lines on each side of the head with postorbital spot area, and number of temporal lines on each side of the head with subocular spot area were primarily responsible for separating most of the Arkansas, Catahoula Parish, and Sabine River populations from the rest of the group. The Sabine River population and the South

Table 12.—Pairwise Mahalanobis' distances (untransformed head pattern area, number of lines, and postorbital blotch connections, with dorsal head area and carapace length as covariates) between nine populations of *G. ouachitensis*: Pop. 1, Wisconsin males and females; Pop. 2, Illinois; Pop. 3, Indiana; Pop. 4, Kentucky; Pop. 5, West Virginia; Pop. 6, Arkansas; Pop. 7, Oklahoma, Lake Texoma; Pop. 8, Louisiana, Catahoula Parish; Pop. 9, Louisiana, Sabine River.

	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5	Pop. 6	Pop. 7	Pop. 8	Pop. 9
Pop. 1	0.0								
Pop. 2	2.3	0.0							
Pop. 3	4.1	2.5	0.0						
Pop. 4	4.3	2.8	2.7	0.0					
Pop. 5	4.7	3.9	3.2	4.8	0.0				
Pop. 6	2.7	1.8	2.2	2.6	4.2	0.0			
Pop. 7	3.9	2.9	2.5	2.5	4.7	1.9	0.0		
Pop. 8	1.8	2.1	3.4	3.8	4.6	2.0	3.3	0.0	
Pop. 9	5.1	4.2	4.0	3.5	6.0	3.4	1.9	4.6	0.0

Table 13.—Pairwise Mahalanobis' distances (untransformed all head pattern characters, dorsal head area and carapace length as covariates) between nine populations of *G. pseudogeographica*: Pop. 1, Wisconsin; Pop. 2, South Dakota; Pop. 3, Illinois; Pop. 4, Indiana; Pop. 5, Tennessee, Tiptonville; Pop. 6, Tennessee, Reelfoot Lake; Pop. 7, Arkansas; Pop. 8, Louisiana, Catahoula Parish; Pop. 9, Louisiana, Sabine River.

	Pop. 1	Pop. 2	Pop. 3	Pop. 4	Pop. 5	Pop. 6	Pop. 7	Pop. 8	Pop. 9
Pop. 1	0.0								
Pop. 2	2.5	0.0							
Pop. 3	1.9	1.4	0.0						
Pop. 4	2.2	1.7	1.9	0.0					
Pop. 5	1.6	1.7	1.0	1.9	0.0				
Pop. 6	2.5	2.5	2.4	2.7	2.3	0.0			
Pop. 7	3.0	3.8	3.3	3.3	3.4	2.7	0.0		
Pop. 8	2.5	3.7	3.4	3.4	3.4	2.7	2.2	0.0	
Pop. 9	3.3	4.7	4.3	4.3	4.3	3.4	2.5	1.4	0.0

Dakota population are at opposite extremes for these characters. These populations also represent the extremes in geographic range of the species. Individuals from the Sabine River all have narrow crescents, small subocular spots and no temporal lines breaking the crescent. The South Dakota population has no crescents, larger subocular spots, and an average of five temporal lines entering the orbit. The Catahoula Parish and Arkansas populations are also separated from the other populations by the predominance of narrow complete crescents, but broken crescents and lines entering the orbit also occur in both of these populations. The Reelfoot Lake population is intermediate in this character between the populations to the south and populations to the north (Table 1). It is closest to the Tiptonville population both in Mahalanobis' distance (Table 13) and geographic distance. The Reelfoot Lake population has a wide variety of head patterns, including crescents and up to eight lines entering the orbit. The Wisconsin population has the narrowest postorbital spots and the smallest mandibular spots, whereas the Reelfoot Lake population has the largest, so large that individuals from that population are difficult to distinguish from *G. ouachitensis* on head markings alone.

Shell pattern.—Although some of the ten carapace pattern categories (Table 6) are more common in certain populations of one or the other species, no differences were found that consistently separate species. Carapace patterns of Sabine River *G. ouachitensis* were similar to those found in other populations of *G. ouachitensis*; however, the frequency of turtles having concentric light colored rings on each scute was nearly 50%. This character state was uncommon in other populations of *G. ouachitensis*. The carapace patterns of *G. caglei* and *G. versa* are similar to the concentric ring pattern found in Sabine River *G. ouachitensis*.

The nine categories of plastral patterns (Table 6) show no consistent differences between the species throughout their distributions. The amount of the plastron covered by dark markings is not a diagnostic character throughout the range of either species. Southern populations of *G. pseudogeographica* often have a high percentage of individuals with plastral patterns that follow the sutures. The plastron of Sabine River *G. ouachitensis* often (17.8% of specimens examined) is marked with a concentric central figure similar to that of *Chrysemys picta belli*. All of the *G. caglei* examined had the plastral pattern, when visible, primarily following the sutures. Larger individuals developed scattered black flecking. This flecking also occurred in many Sabine River *G. ouachitensis*. The plastrons of 77

G. versa were primarily unmarked yellow (91.8%); the remaining (8.2%) were mottled yellow brown.

DISCUSSION AND CONCLUSIONS

After examination of a large number of *Graptemys* from the Mississippi River at Stoddard, Wisconsin, a review of the taxonomic literature on the *G. pseudogeographica* complex, and examination of museum specimens from other localities, I concluded that the characters previously used for diagnosing taxa in the complex were not reliable.

Canonical analysis of head patterns alone did not completely separate *G. pseudogeographica* and *G. ouachitensis*. As in Darwin's Finches, there is considerable overlap between the species when the patterns of all populations are compared simultaneously. Presence or absence of a postorbital crescent, or the number of lines entering the orbit were not useful in sorting individuals to species. However, these characters did separate the two species in sympatric populations and subspecies within each species.

The size of the postorbital, subocular, and mandibular spots was most important in separating *G. ouachitensis* from *G. pseudogeographica*, regardless of the number of temporal lines entering the orbit. The combination of temporal lines and size of spots makes certain separation possible at most localities.

Reduced postorbital spots, transverse chin bars, and a large number of lines entering the orbit ($\bar{x} = 6.5$) separate over 75% of the Sabine River *G. ouachitensis* from other populations of *G. ouachitensis* studied. Since the Sabine River population is also geographically isolated, its status as a subspecies, *G. ouachitensis sabinensis*, is justified. Some individuals in this population that are indistinguishable from *G. o. ouachitensis* in head pattern are considered intergrades.

Populations of *G. pseudogeographica* from Arkansas, Catahoula Parish, Louisiana, and the Sabine River are separated from other populations of *G. pseudogeographica* primarily on the basis of fewer lines entering the orbit and smaller postorbital spots. Populations of *G. pseudogeographica* from the Sabine River and South Dakota, at the extremes of the species' geographic range, exhibit opposite extremes in head pattern. The Sabine River turtles have narrow postorbital crescents and small subocular spots, and never have any lines breaking the crescents. The Mahalanobis' distance of 4.66 between these two populations suggests that there is less than a 10% overlap between them.

The data in Table 13 show that *G. pseudogeographica* populations from Wisconsin, South Dakota, Illinois, Indiana, and Tiptonville, Tennessee, are similar. I refer these populations to the subspecies *G. pseudogeographica pseudogeographica*. All of these populations are close to at least two other populations in the group (distance of less than two standard deviations). The Arkansas, Catahoula Parish, Louisiana, and Sabine River populations have Mahalanobis' distances closer to each other than to any other group. I regard these populations as constituting the subspecies *G. pseudogeographica kohni*. The Reelfoot Lake population is intermediate between northern and southern populations. The Mahalanobis' distances between Reelfoot Lake and Arkansas, and Reelfoot Lake and Indiana are equal: 2.66. It is a geographically intermediate population wherein the subspecies *G. pseudogeographica pseudogeographica* and *G. pseudogeographica kohni* intergrade, as in other populations in Missouri and Illinois. I recognize the northern and southern populations of *G. pseudogeographica* as subspecies, even though they represent the ends of a cline in variation.

Incubation of clutches of eggs from known females at several different tem-

peratures clarified the limits of head pattern variability. No clutches were found with hatchlings so different from the female parent that they might be considered interspecific hybrids. In addition, all female *G. ouachitensis* which had particularly small postorbital and subocular spots, suggesting possible hybridization with *G. pseudogeographica*, produced offspring that were clearly *G. ouachitensis*. The influence of incubation temperature on the size of the postorbital, subocular, and mandibular spots and on the number of temporal lines entering the orbit helps to explain intraspecific variation at a locality and emphasizes the need to examine large samples before arriving at taxonomic conclusions in this group.

Osteological comparisons showed *G. ouachitensis* and *G. pseudogeographica* males and females from both northern and southern localities to be closer to each other than to either *G. geographica* or *G. versa*.

Both shell and skull shape are important in separating *G. geographica* from the *G. pseudogeographica* complex. *Graptemys pseudogeographica kohni* females are closer to the *G. geographica* group than to any other population of *Graptemys* examined, due to their wide, massive skulls and great dentary widths. When only females from each population were used for analysis, *G. geographica* females were clearly removed from the *G. pseudogeographica* complex by the ratios of postpalatal foramen width to pterygoid width and plastron width to intersquamosal width. Differences in the skeletal characters of Wisconsin specimens substantiated separation of *G. pseudogeographica* and *G. ouachitensis*. Skeletal differences between southern and northern populations of *G. ouachitensis* were greater than between *G. pseudogeographica* populations. The ratios of dentary width to carapace height and plastron width to pterygoid width separated *G. ouachitensis* from *G. pseudogeographica*. These measurements emphasized the wider jaws and plastron of *G. pseudogeographica* and the higher carapace of *G. ouachitensis*. At Stoddard the two species were separated by 4.4 standard deviations primarily by the different ratio of dentary width to pterygoid width. When skeletal features were combined with head pattern characters, the Wisconsin population of *G. ouachitensis* was separated from sympatric *G. pseudogeographica* by a distance of 11 standard deviations. The contrasts between carapace width and size of the mandibular spot, and plastron width and maximum skull width were mainly responsible for the separation.

Several factors may help to explain the divergence of skull size in southern and northern populations of *Graptemys*. *Graptemys geographica* occurs with *G. ouachitensis* and *G. pseudogeographica* at the Wisconsin site, but not at the southern localities studied. A study of food partitioning (Vogt, 1981b) showed that *G. geographica* is a mollusk specialist in Wisconsin and has a 0.21 niche overlap with *G. ouachitensis*, whereas *Graptemys pseudogeographica* and *G. ouachitensis* in the same community have a 0.76 overlap. Competition with *G. geographica* is absent in southern turtle communities, where the species does not occur. However, the generalist *Trachemys scripta* and the herbivore *Pseudemys concinna* are abundant. In the South, *G. pseudogeographica kohni* is a mollusk specialist, developing wide crushing surfaces on the jaws as a consequence of this dietary preference. Southern *G. ouachitensis* are more insectivorous and restricted to fast-moving portions of rivers, thus avoiding competition with *T. scripta* which occurs in oxbow ponds and slower reaches (McCoy and Vogt, in preparation).

Berry (1975) observed character convergence where large-headed *Sternotherus minor* was sympatric with the narrow-headed *S. odoratus*. He suggested this was the result of competition for a limited food resource. He found the larger species, *S. minor*, becoming smaller in the presence of the small congener. In Wisconsin,

G. pseudogeographica has been displaced as a mollusk specialist by *G. geographica* and is under selection for a head size most efficient at being a generalist (Vogt, 1980b). Since *G. pseudogeographica* and *G. ouachitensis* in that population overlap considerably in the types of food eaten, (primarily insect larvae and vegetation [Vogt, 1981b]) they have converged in head size. Absence of competition from *Trachemys* (which is an opportunist, feeding on insects, mollusks, plants, fungi, and carrion) probably permitted the evolution, in Wisconsin, of larger *G. ouachitensis* that are more capable of utilizing a generalized food resource.

Shell patterns were compared and found not to be useful taxonomic characters throughout the geographic ranges of the two species, although at specific localities plastral patterns of hatchlings were useful in separating *G. pseudogeographica* from *G. ouachitensis*.

Electrophoretic comparison of proteins is not as useful for distinguishing lower taxonomic categories of emydid turtles as it is in some other vertebrates (Selander and Johnson, 1973). I found no discrete differences between subspecies, and few at the species level. As a taxonomic tool below the generic level, electrophoresis should be used with extreme caution. Merkle (1975) found striking similarities in 17 protein systems in the genus *Clemmys*, where at least 10 systems were shared between all four species and only three separated *C. muhlenbergi* from *C. guttata* and two separated the subspecies *C. m. marmorata* from *C. marmorata pallida*. McKown (1972) found electrophoresis of blood proteins in both *Graptemys* and *Malaclemys* to be inadequate for elucidating phylogenetic relationships below the generic level. Only two of the 19 protein systems that I examined electrophoretically showed intra- or interspecific variation between populations of *G. ouachitensis* and *G. pseudogeographica*. Relative mobility differences in plasma esterase (P-EST, Table 8) were small though consistent, and showed phenotypic similarities between *G. ouachitensis sabinensis* and *G. o. ouachitensis* as well as among populations of *G. pseudogeographica*. However, differences between populations of *G. o. ouachitensis* were as great as or greater than differences between sympatric populations of *G. ouachitensis* and *G. pseudogeographica*. The only heterozygous locus, MDH-3, showed inconsistent frequencies of allozyme distributions in the three populations of *G. ouachitensis* and the two populations of *G. pseudogeographica* studied (Table 9, Table 10). However, the predominance of the cc phenotype in both populations of *G. pseudogeographica* compared to sympatric *G. ouachitensis* provided evidence that *G. pseudogeographica* from Wisconsin is conspecific with the Arkansas population. Furthermore, *G. ouachitensis* from the Sabine River possessed allozyme frequencies similar to those of the other populations of *G. ouachitensis*, supporting their status as conspecific. Although electrophoresis did not give discrete separation between the species examined, it was useful in indicating relationships.

Differences in courtship behavior further support separating *G. ouachitensis* and *G. pseudogeographica* as species. There are species-specific differences in the number of times the foreclaws are drummed against the ocular regions of the female per titillation bout (5.2 vs. 10.3). Head bobbing during titillation by both subspecies of *G. pseudogeographica*, but not by *G. ouachitensis*, also differentiates the species.

Males apparently recognize conspecific females by both visual and olfactory cues, as males did not court freeze-dried conspecific females. Auffenberg (1965) found cloacal secretions to be important in recognition of conspecifics in *Geochelone*. However, field experiments with *Chrysemys picta* (Vogt, 1980c) failed to demonstrate that females release species-specific pheromones to attract males

in that emydine species. Preliminary laboratory observations of precopulatory or precourting *Graptemys* suggests that species-specific odors are present, but further experiments are needed.

The combination of data confirms that *G. pseudogeographica* and *G. ouachitensis* are separate species, each with two subspecies: *G. pseudogeographica pseudogeographica* and *G. pseudogeographica kohni*; *G. ouachitensis ouachitensis* and *G. ouachitensis sabinensis*. *Graptemys versa* is more distant from the *G. pseudogeographica* complex than is *G. geographica* as shown by skeletal anatomy. *Graptemys caglei* is thought to be related to *G. ouachitensis* on the basis of head and shell patterns. My interpretation is that the allopatric *G. caglei* and *G. versa* are distinct species, which are provisionally retained in the *G. pseudogeographica* complex pending further study.

SYSTEMATIC ACCOUNTS

Graptemys ouachitensis Cagle

Fig. 12 a–l; Fig. 13a–l; Fig. 15a–f; Fig. 16; Fig. 19

Graptemys pseudogeographica ouachitensis Cagle, 1953:10. Type locality: Ouachita River, four miles northeast of Harrisonburg, Catahoula Parish, Louisiana. Holotype, UMMZ 104345.

Malaclemys pseudogeographica ouachitensis: Cochran and Goin, 1970:149.

Graptemys ouachitensis: Vogt, 1980b:18. First use of present combination.

Definition. — *Graptemys ouachitensis* is a medium-sized emydid turtle: females reach 26 cm in carapace length, males 16 cm. The carapace is elevated with low black knobs on the second, third, and fourth vertebrals. The plastron is flat. The carapace is green with one to six, usually one, black blotch on the posterior border of each scute. The blotches are encircled with yellow or orange, or a lattice of interconnected circles may be present without the black blotches. The pattern is often faded in adults and melanism is frequent in northern populations. The cream to yellow plastron is marked with dark concentric swirls of alternating yellow and dark green; the green may be reduced to lines following the sutures. The pattern covers less than 50% of the plastron. This pattern fades to brown-yellow mottling in adults and is replaced by dark lines along the sutures. The head is dark green with yellow markings. A large postorbital spot extends from under the orbit around the posterior border to meet a pair of longitudinal narrow lines running the length of the head (Fig. 12a, b; Fig. 13a, b, d, e). This crescent may be broken behind the eye, and there may be 1–9 wide stripes entering the orbit (Fig. 12k; Fig. 13h, i; Fig. 15b, d, e, f). The spot below the orbit is large, and directly below this spot is a large yellow spot on the lower jaw (Fig. 12e, h, k; Fig. 13h, i). Four large yellow spots (one at the symphysis, one on each mandible, and one in the center), or alternating yellow and dark green transverse bars (Fig. 13c; Fig. 15c) mark the underside of the head.

Distribution. — *Graptemys ouachitensis ouachitensis* occurs from the Mississippi and St. Croix rivers in Minnesota and Wisconsin south in the Mississippi River Basin through Louisiana. It is found as far west as Lake Texoma, Oklahoma (Red River), and east into Indiana and West Virginia. *Graptemys ouachitensis sabinensis* is restricted to the Sabine River Drainage of Louisiana and Texas (Fig. 16).

Graptemys ouachitensis ouachitensis Cagle

Graptemys pseudogeographica ouachitensis Cagle, 1953:10.

Graptemys ouachitensis ouachitensis: Vogt, 1980b:107. First use of present combination.

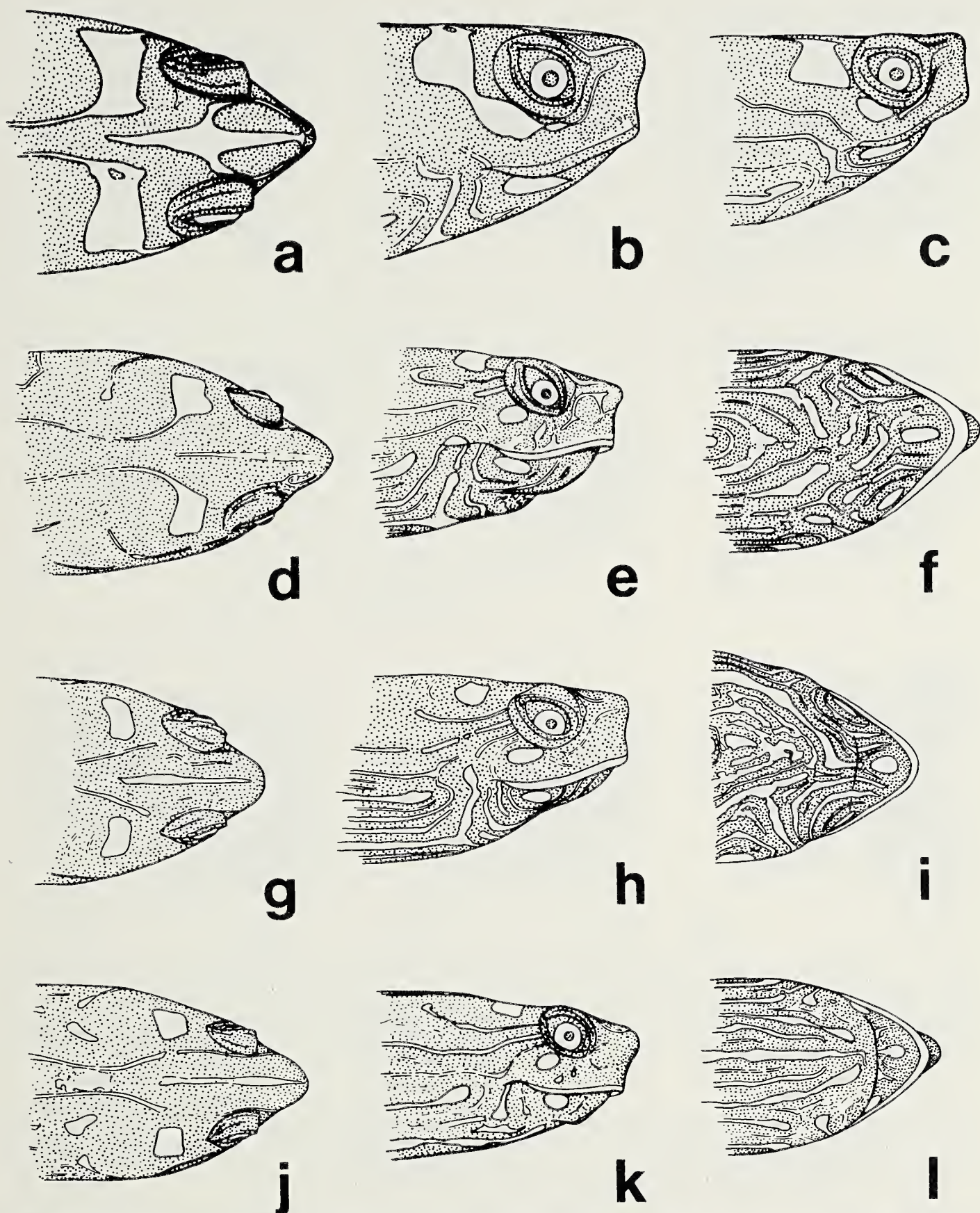


Fig. 12.— Variation in head pattern of *G. o. ouachitensis* from Stoddard, Vernon Co., Wisconsin (RCV field numbers 354, 394, 488, 537, 561) showing the maximum (a–b) and minimum (j–k) sizes of postorbital and subocular spots in northern populations.

Definition.—*Graptemys ouachitensis ouachitensis* reaches largest size in the northern United States. The postorbital spot is usually large, rarely reduced, and never has narrow yellow rings around it (Fig. 12d, e, g, h, j, k). The postorbital spot may be enlarged and connected with the subocular spot to form a wide crescent (Fig. 12a, b). This is more common in northern populations than in

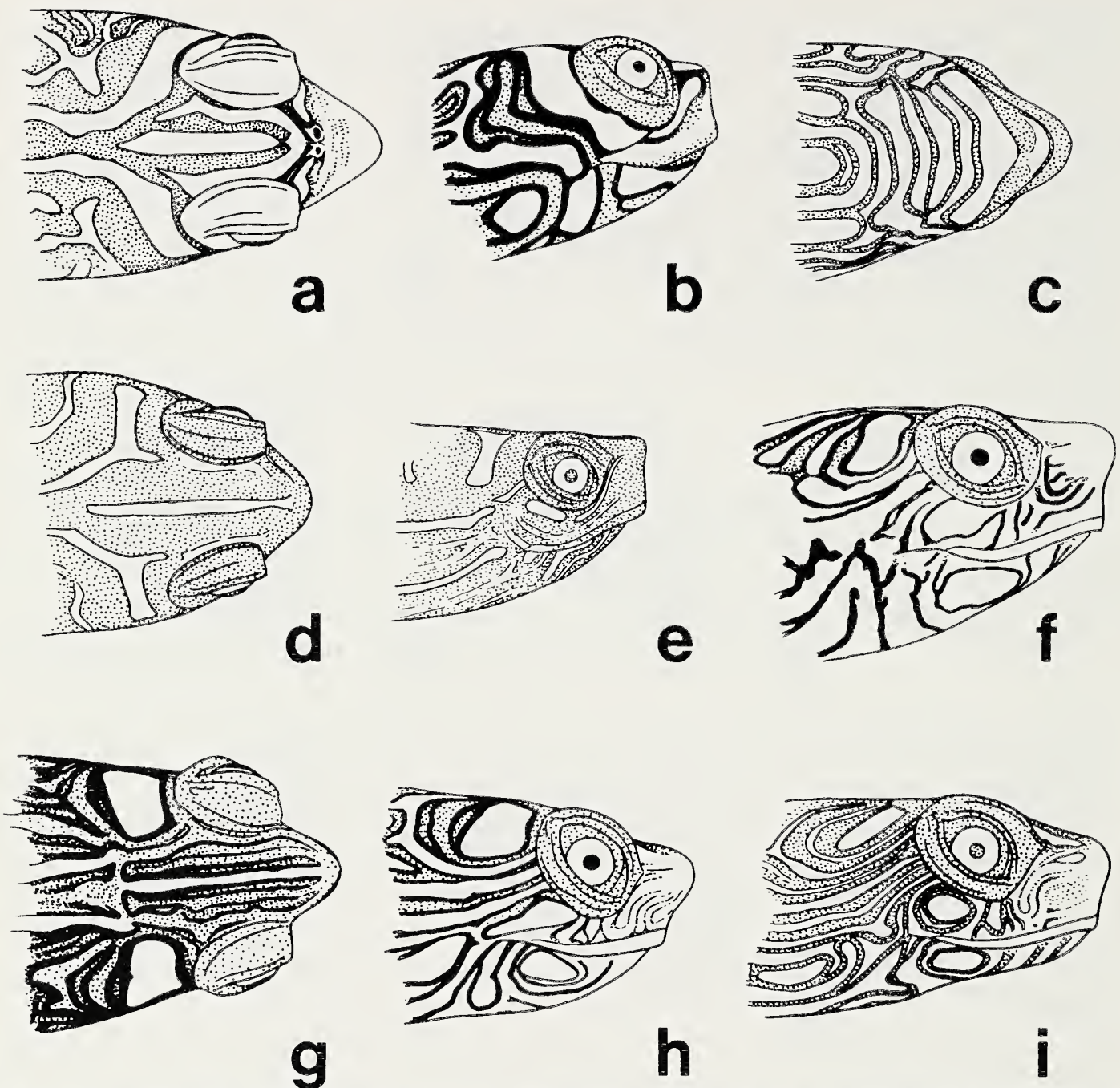


Fig. 13.—Variation in head pattern of *G. o. ouachitensis* showing the maximum (a–b), intermediate (d–h), and minimum (i) sizes of postorbital and subocular spots in southern populations. Localities as follows: a–e (TU 12535, 12658, Louisiana, Catahoula Par.; Ouachita R., 4 mi N Harrisonburg); f–i (TU 16937, 16937.1–16937.2, Tennessee, Perry Co., Tennessee R., between Saltillo and Dunville).

southern populations. The underside of the head usually has four large spots, and is rarely cross-banded (Fig. 12f, i, l). The plastral pattern usually covers less than 75% of the shell and is often restricted to the sutures.

Graptemys ouachitensis sabinensis

Cagle, new combination

Graptemys pseudogeographica sabinensis Cagle, 1953:2. Type locality: Sabine River, eight miles southwest of Negreet, Sabine Parish, Louisiana. Holotype, UMMZ 104351.

Malaclemys pseudogeographica sabinensis: Cochran and Goin, 1970:149.

Definition.—Smaller in carapace length, *G. ouachitensis sabinensis* males reach 8 cm in length and females 12 cm. The postorbital yellow marking is reduced to a spot in most individuals (Fig. 15a, b, d). Six to nine yellow lines enter the orbit on each side of the head (Fig. 15b, d, e, f). At least four of these lines are wide. The throat is marked with transverse alternating yellow and dark green bars (Fig.

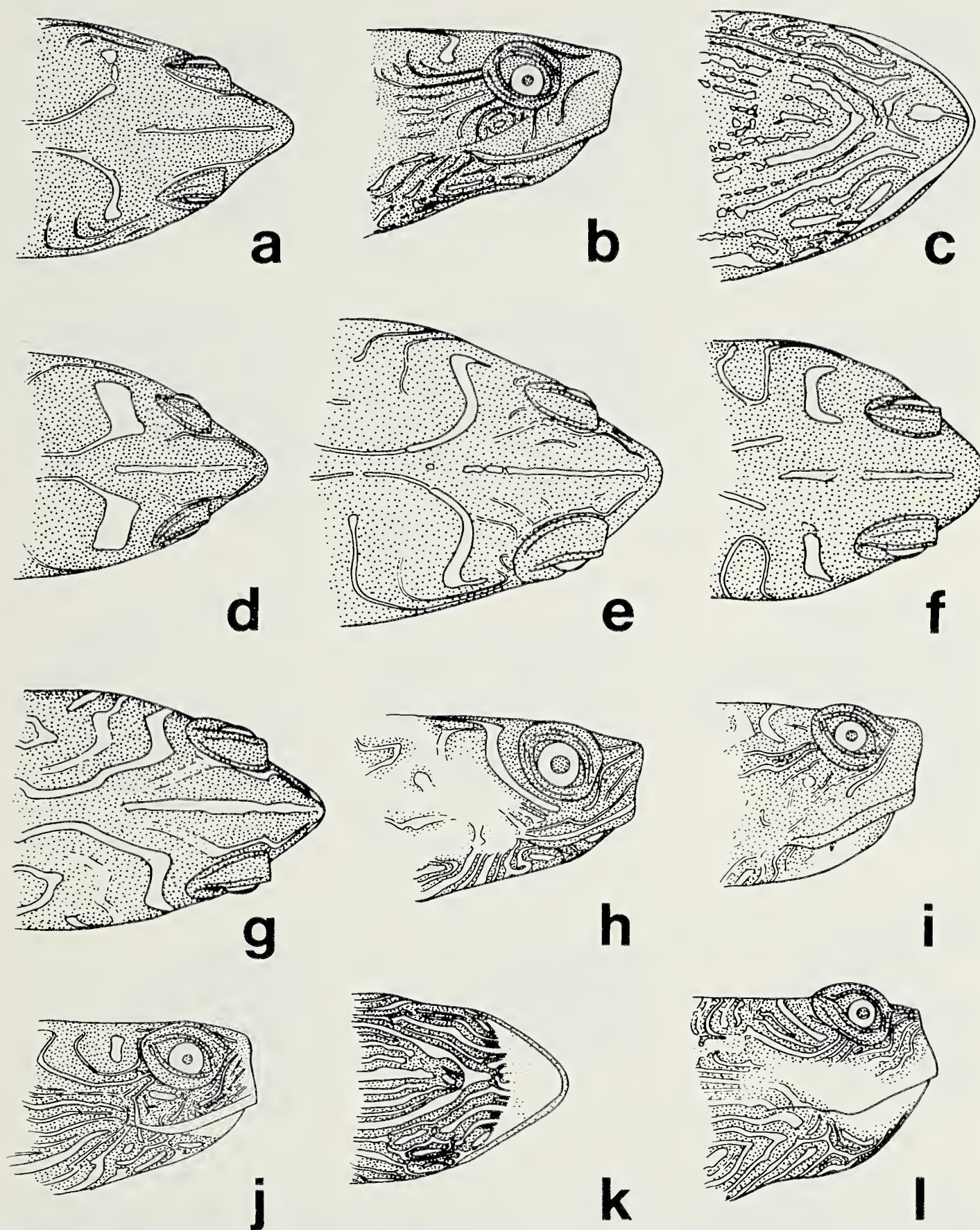


Fig. 14.—Variation in head pattern of *G. pseudogeographica*. Localities as follows: a–f (RCV field numbers 417, 443, 508) *G. p. pseudogeographica* from Stoddard, Vernon Co., Wisconsin, showing minimum (a–b) and maximum (d) sizes of postorbital and subocular spots, and postorbital crescent (f); *G. pseudogeographica kohni* g–h (CM 4258, 4259, Louisiana, Caddo Par., Red R., 1 mi W Gayle); i (MAZG 1465, Louisiana, Ouachita Par., Ouachita R., 15 mi SE Monroe); j–k (USNM 100243, Louisiana, Iberville Par., Plaquemine); l (CM 4257) same as g–h.

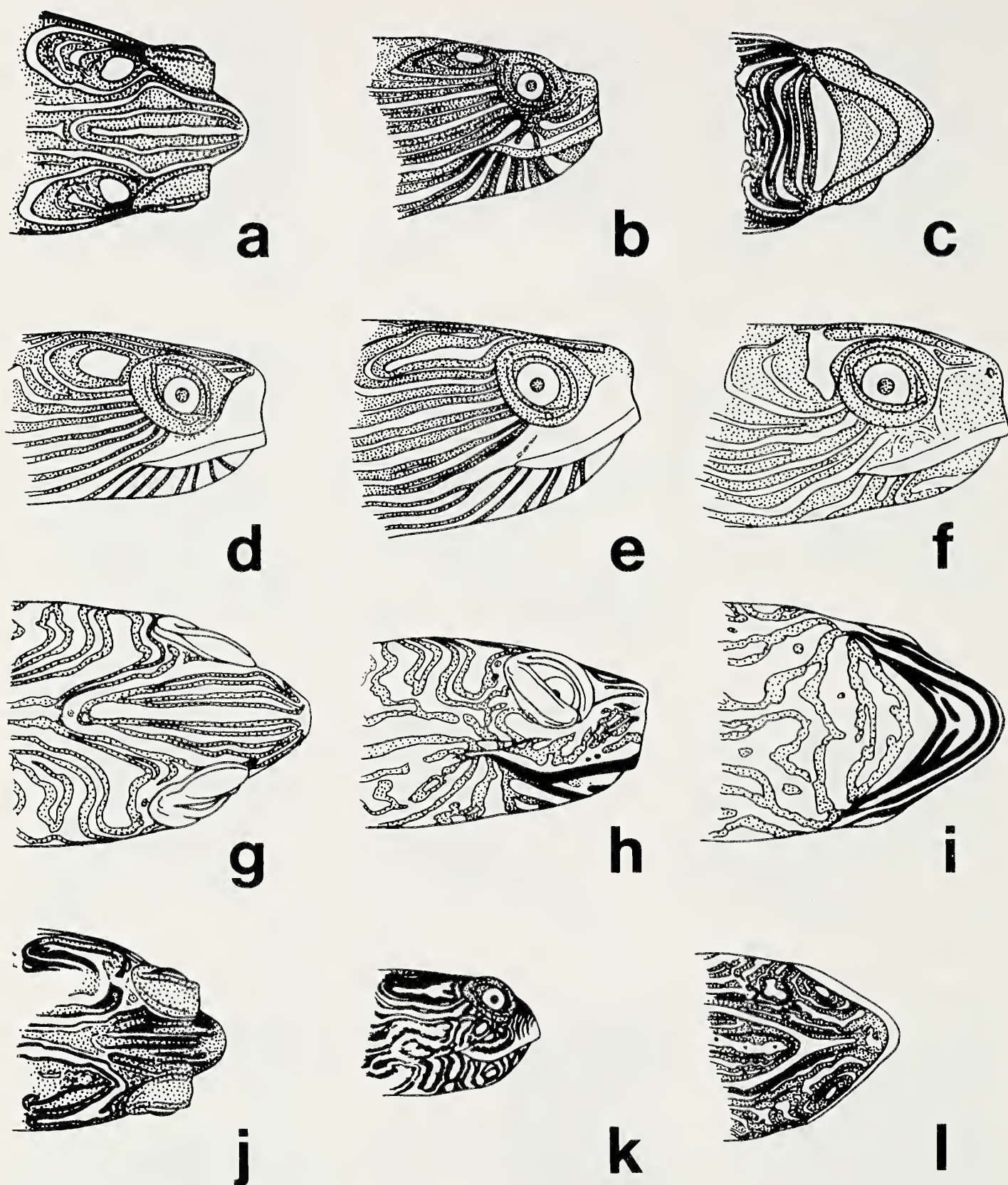


Fig. 15.— Variation in head pattern of *G. ouachitensis sabinensis*, *G. caglei*, and *G. versa*. *G. ouachitensis sabinensis*: a–f (UMMZ 104356; TU 13760.11, 13760.30, 13760.35; Louisiana, Sabine Par., 8 mi SW Negreet). *G. caglei*: g–i (MCZ 16767, Texas, DeWitt Co., Guadalupe R.). *G. versa*: j–l (SMBU 5084, Texas, Kimble Co., 3 mi SE Telegraph, Paint Rock Ranch).

15c). The central two thirds of the plastron is marked with yellow and dark green reticulations. The plastron of males is often flecked with black.

Graptemys pseudogeographica (Gray)

Fig. 14a–l; Fig. 17; Fig. 18

Emys pseudogeographica Gray, 1831:341. Type locality: Wabash River, New Harmony, Posey County, Indiana. Lectotype, MNHN 9147 (Bour and Dubois, 1983).

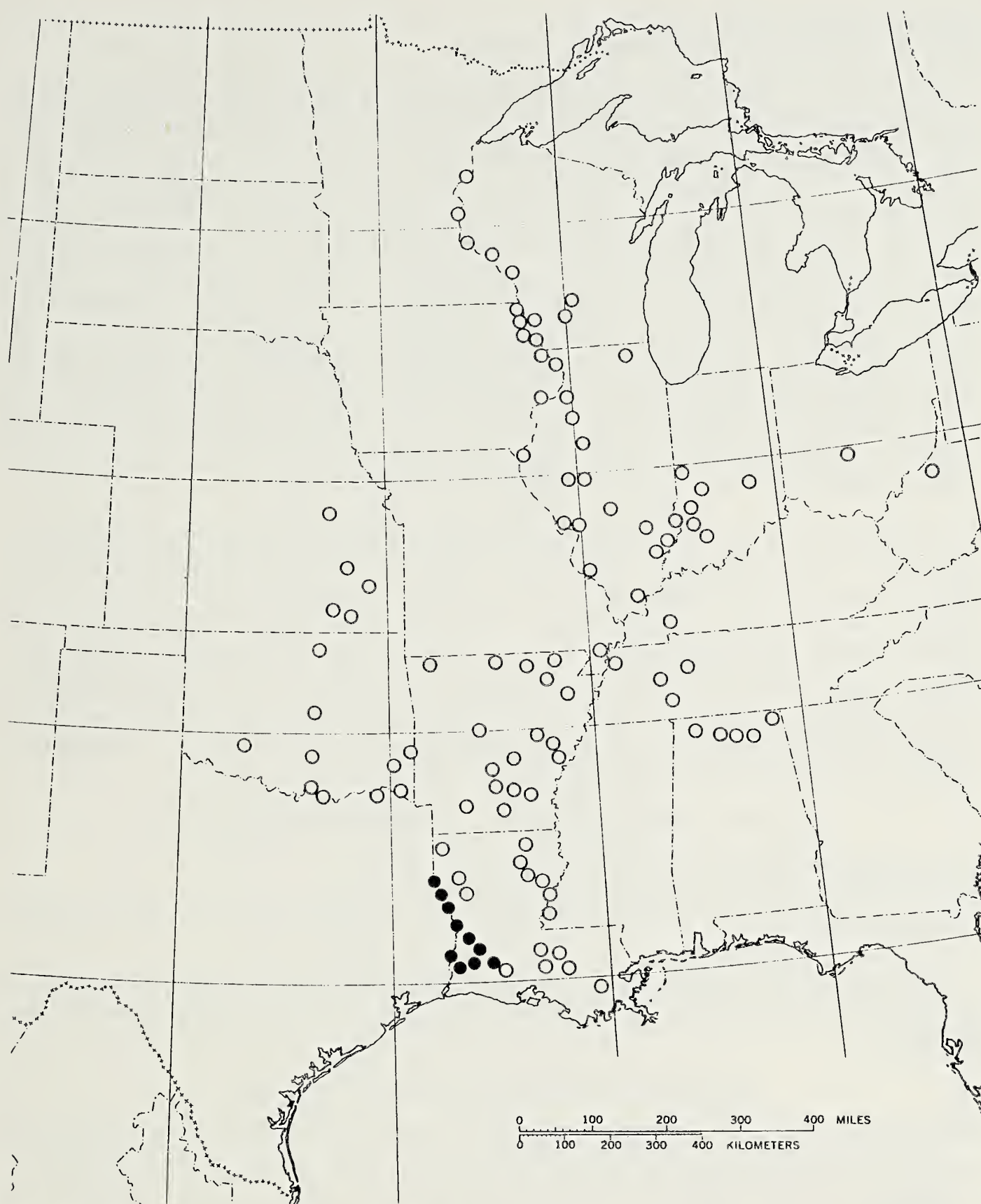


Fig. 16.—Map showing localities from which specimens of *G. o. ouachitensis* (open circles) and *G. ouachitensis sabinensis* (solid circles) were examined.

Emys lesueurii Gray, 1831:31. Type locality: Wabash River, New Harmony, Posey County, Indiana.

Emys geographica (part): Duméril and Bibron, 1835:256.

Graptemys lesueurii: Agassiz, 1857:436.

Graptemys pseudogeographica: Gray, 1863:180. First use of present combination.

Clemmys pseudogeographica: Strauch, 1862:33.

Malacoclemmys pseudogeographica: Cope, 1875:53.

Malacoclemmys lesueuri: Yarrow, 1882:34.

Malacoclemmys pseudo-geographicus: Davis and Rice, 1883:32.

Graptemys pseudogeographicus: Paulmier, 1902:393.

Malaclemys lesueuri: Hurter, 1911:243.

Malaclemys pseudogeographica: McDowell, 1964:274.

Definition. — *Graptemys pseudogeographica* is a medium-sized emydid, female carapace length to 27.7 cm, male to 15 cm, with an elevated carapace having low black knobs on the second, third, and fourth vertebrae. The plastron is marked with dark concentric swirls of alternating yellow and dark green. In adult females the plastron color fades to a yellow-brown mottling. The skull becomes greatly widened in large females in some southern populations. The carapace is olive green, usually with one dark blotch on the posterior border of each scute. Blotches are encircled with yellow or orange; this pattern is often faded in adults. The pattern may have as many as six encircled blotches, or no blotches with only an interconnected orange lattice. The head markings range from a complete narrow yellow-orange crescent posterior to the orbit (Fig. 14g) to a broken crescent with one to six lines entering the orbit (Fig. 14b, f, i, j, l). The underside of the jaw is marked with longitudinal alternating yellow and green lines (Fig. 14c, k). Anteriorly, these lines break up into a highly variable pattern.

Distribution. — *Graptemys pseudogeographica* is found primarily in large drainages of the Mississippi River Basin, from the St. Croix and Wisconsin rivers in northern and central Wisconsin and the upper Mississippi River in Minnesota through Louisiana and eastern Texas. The range follows the Missouri River into North Dakota and extends east to the western edge of Tennessee, Kentucky, Indiana, and central Ohio. Fig. 17 shows the range of *G. pseudogeographica pseudogeographica* in the north and *G. pseudogeographica kohni* in the south with a zone of intergradation in southern Illinois, southern Missouri, northeastern Arkansas and the western tips of Kentucky and Tennessee.

Graptemys pseudogeographica pseudogeographica (Gray)

Emys pseudogeographica Gray, 1831: 31. See species synonymy.

Emys lesuerii Gray, 1831:31. See species synonymy.

Graptemys pseudogeographica pseudogeographica: Stejneger and Barbour, 1917:117. First use of combination.

Definition. — This subspecies is characterized by having 3–6 temporal lines entering the orbit (Fig. 14b). Megacephalic females are rare in populations of this subspecies.

Graptemys pseudogeographica kohni (Baur)

Malacoclemmys kohni Baur, 1890:263. Type locality: Bayou Lafourch, Bayou Teche, and St. Martinsville, Louisiana. Type specimen unknown.

Graptemys pseudogeographica kohni: Stejneger and Barbour, 1917:117. First use of present combination.

Graptemys kohni: Cagle, 1954:181.

Malaclemys kohni: McDowell, 1964:274.

Definition. — This subspecies is characterized by having complete postorbital crescents (postorbital spot joined with the subocular spot, Fig. 14g), or one (Fig. 14f) to three (Fig. 14i, j) temporal lines entering the orbit. Megacephalic females are common in many populations.

G. caglei Haynes and McKown

Fig. 15g–i

Graptemys caglei Haynes and McKown, 1974:173. Type locality: Guadalupe R., 8 km NW Cuero, DeWitt Co., Texas. Holotype, TNHC 36061.

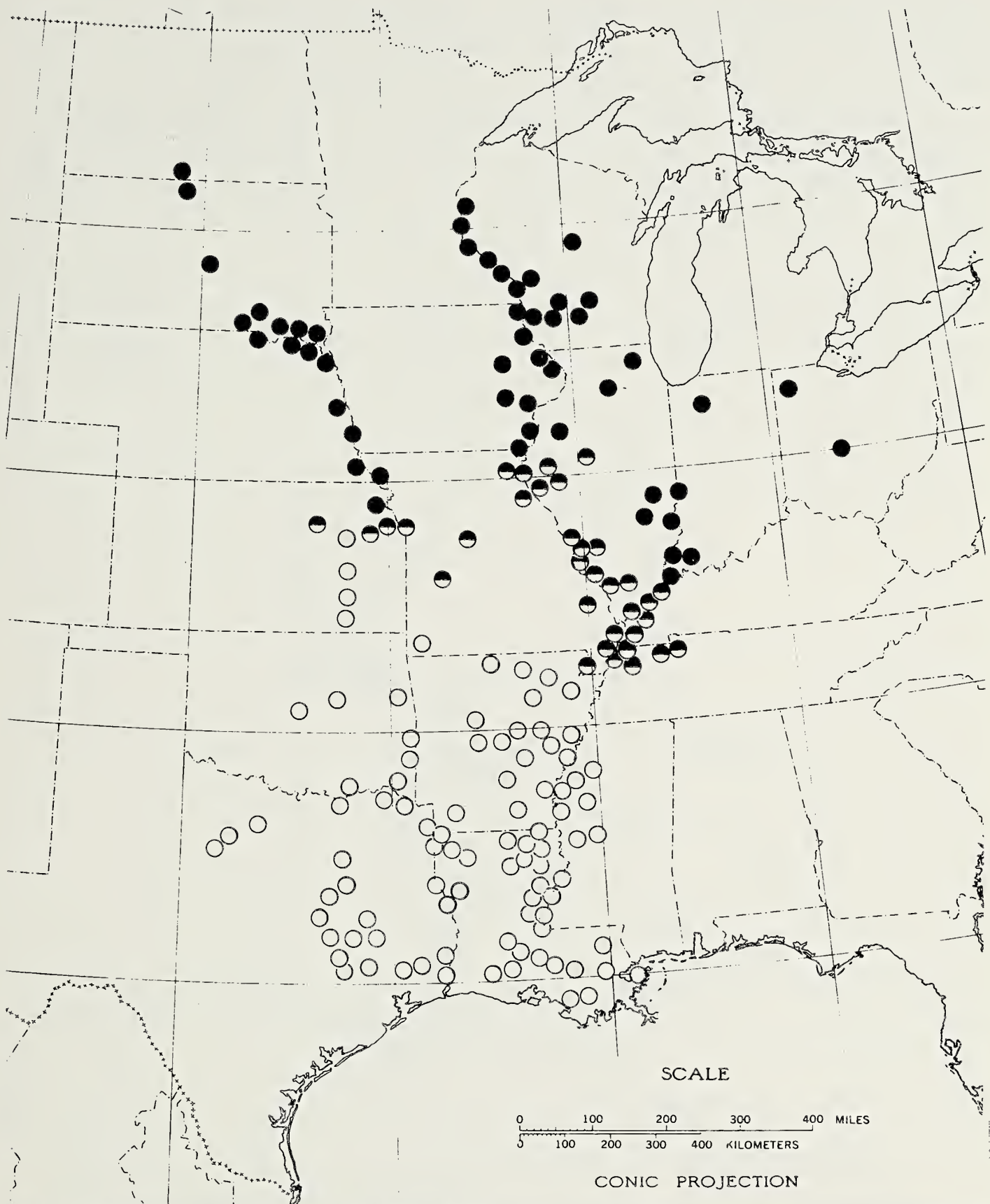


Fig. 17.—Map showing localities from which specimens of *G. p. pseudogeographica* (solid circles), *G. pseudogeographica kohni* (open circles), and intergrades (half open circles) were examined.

Definition.—*Graptemys caglei* is a medium-sized emydid: males reach 11 cm carapace length and females 16 cm carapace length. The carapace has a middorsal keel with sharp vertebral spines. The carapace is light green with cream-colored circular lines on the pleurals and marginals. The cream-colored plastron is heavily flecked with black and black lines extend along the seams. The head is black with cream stripes. Single postorbital crescents on each side extend to meet on the dorsal midline behind the orbits. The ventral side of the jaw has a transverse line.

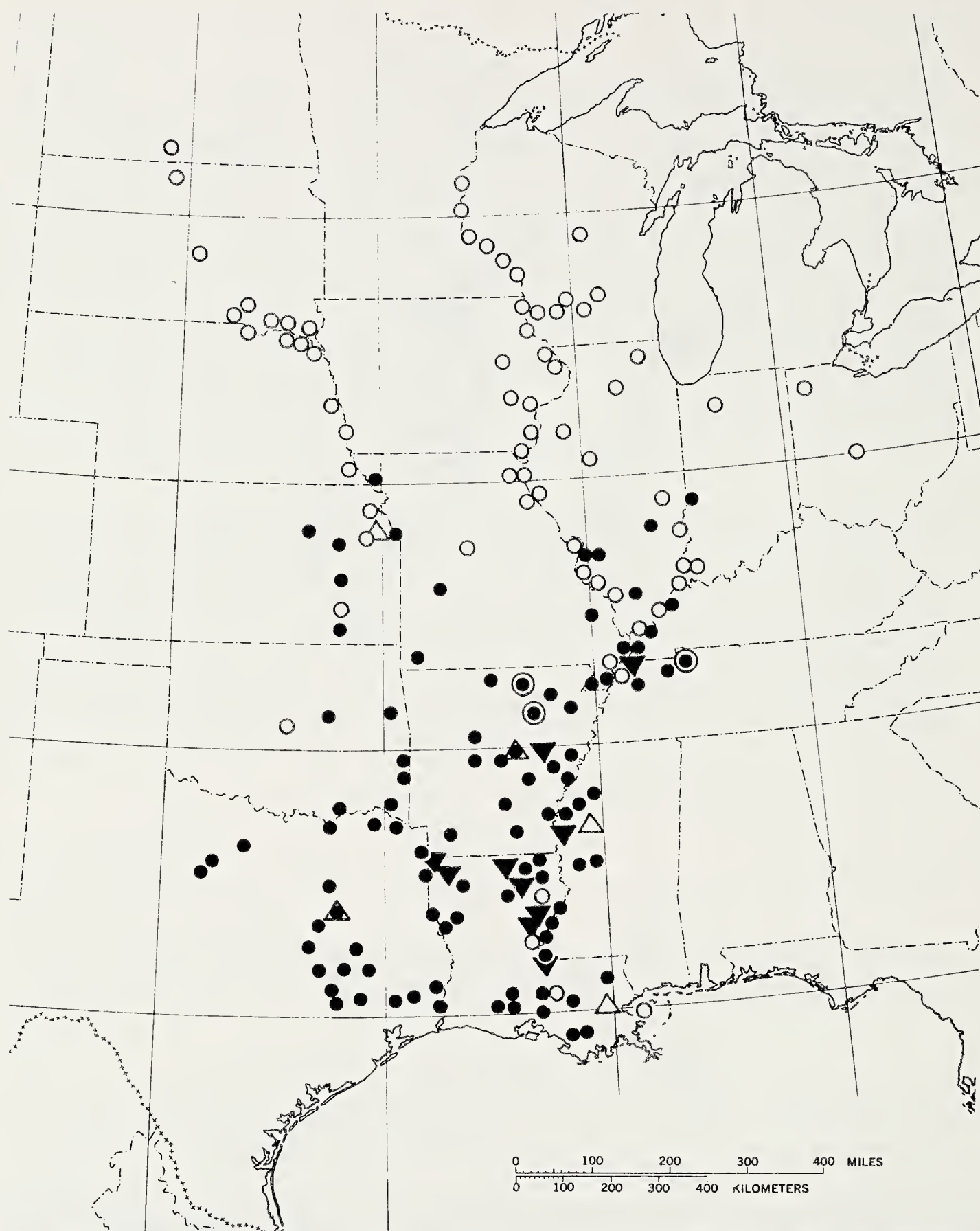


Fig. 18.—Map showing locations of populations of *G. pseudogeographica* in which individuals had the following head pattern characters: complete crescents (solid circles); incomplete crescents (triangles); incomplete crescents with lines entering orbit (open circles); all three of the preceding (inverted triangles); complete crescents and lines entering orbit (concentric circles).

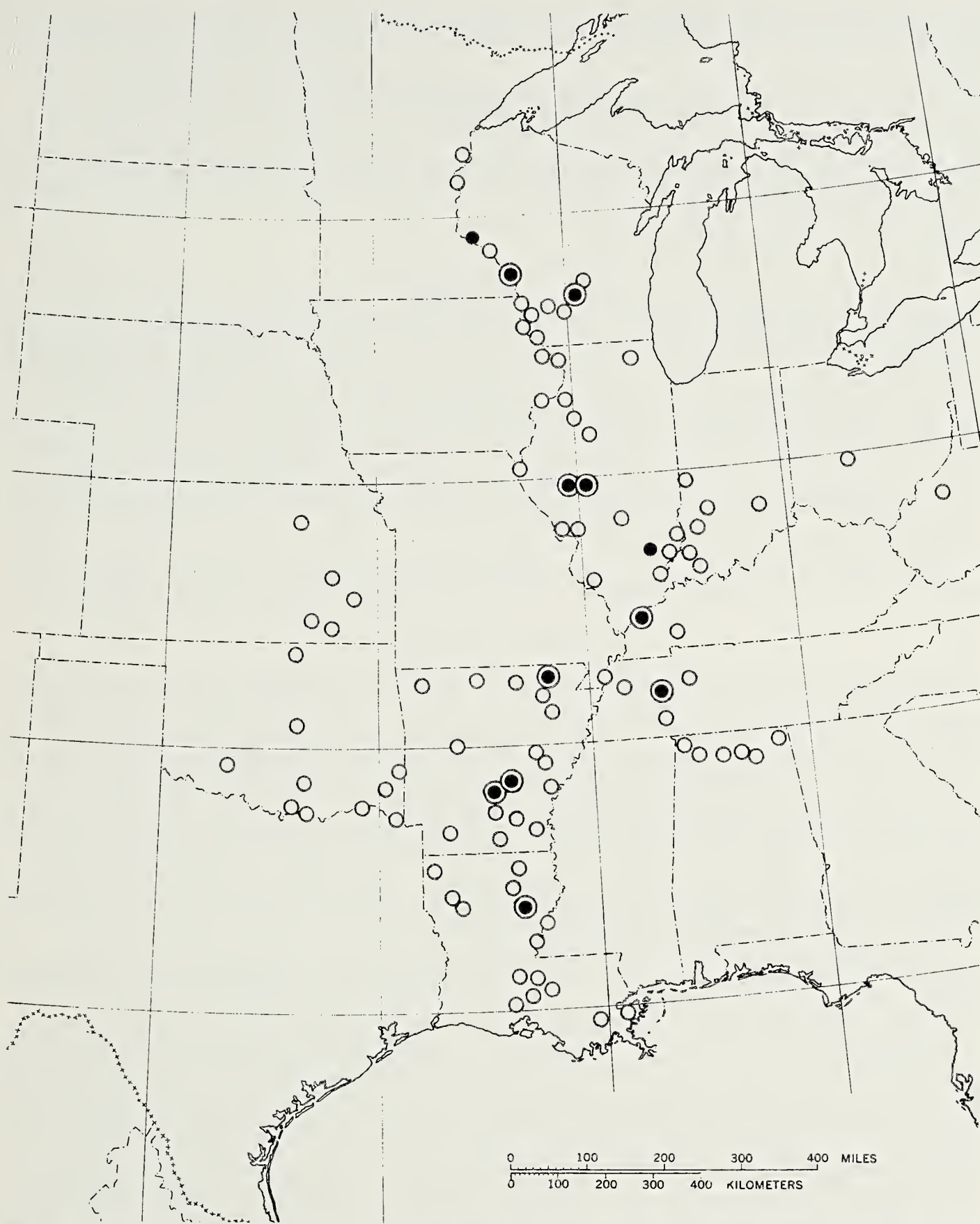


Fig. 19.—Map showing locations of populations of *G. ouachitensis* in which individuals had either complete postorbital crescents (solid circles), or incomplete postorbital crescents (open circles), or both (concentric circles).

Distribution.—The Guadalupe River system, southcentral Texas (map in Haynes, 1976).

Gratemys versa Stejneger
Fig. 15j-l

Gratemys pseudogeographica versa Stejneger, 1925:463. Type locality: Austin, Travis Co., Texas.

Holotype, USNM 27473 (Vogt, 1981c).

Gratemys versa: Smith, 1946:60. First use of present combination.

Malaclemys versa: McDowell, 1964:274.

Definition.—*Gratemys versa* is a medium-sized emydid: females reach 18.3 cm carapace length and males 11 cm. Distinct knobs are not present along the dorsal keel. The carapace is olive green and each scute has one to 20 spots, each consisting of three to four concentric yellow circles with a yellow center. The pattern fades in adults. The yellow plastron has dark lines along the seams. The head is olive green with yellow-orange markings. Usually a distinctly j-shaped mark lies posterior to each orbit, with the hook extending posteriorly. Three to 16 temporal stripes enter the orbit. The lower part of head and neck are patterned with yellow flecks.

Distribution.—*Gratemys versa* occurs in the Colorado River drainage, primarily on the Edwards Plateau of westcentral Texas (map in Vogt, 1981c).

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(UWZM). Specimens designated RCV are deposited in University of Wisconsin–Madison or Carnegie Museum of Natural History. The lectotype of *Emys pseudogeographica* is in the Muséum national d'Histoire naturelle, Paris (MNHN).

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APPENDIX

Specimens examined. Asterisk denotes skeletal specimens, others are fluid preserved. See Acknowledgments for identifications of museum acronyms.

Graptemys caglei.—TEXAS: DeWitt Co., Guadalupe River, TNHC 34067, 36055–36056, 36058, 36061–36065, 36068–36070, 36075–36083, 36085–36087, 36089–36091, 36094–36096, 36098–36102, 36622–36626, 36629; MCZ 16767; CM 61699–61701. Gonzales Co., no specific locality, TNHC 36054. Kerr Co., no specific locality, TNHC 34022–34023.

Graptemys geographica.—MISSOURI: no specific locality, MPM 6120–6130, 6132. WISCONSIN: Vernon Co., Stoddard, Mississippi River, UWZM 21807–21816, 21953, 21955, 21958, 23315*, 23321*, 23329*.

Graptemys ouachitensis ouachitensis.—ALABAMA: Wheeler Reservoir, Tennessee River, USNM 118143–118144. ARKANSAS: *Benton Co.*, White River, NLU 607, 609, 615, 627, 629. *Desha Co.*, White River, near mouth, FMNH 15677; White River, near Mississippi River, FMNH 15718, 15721–15722. *Drew Co.*, Sale River, near Monticello, NLU 21458. *Garland Co.*, Percy, 15 mi from Hot Springs, UIMNH 28858. *Jefferson Co.*, Arkansas River at Pine Bluff Arsenal, CM 23995; USNM 55532. *Lawrence Co.*, Black River, TU 14610(19), 15154*–15159*; Powhatan, FMNH 15243–15244, 15247, 92127, 92129; MCZ 1725, 29087; Black River, 1.5 mi SW Black Rock, FMNH 73295–73297. *Marion Co.*, White River near Cotter, TU 14597. *Monroe Co.*, White River at Clarendon, TU 16854(30), 17109, 17111–17113; Indiana Bay Ferry, CM 24600. *Prairie Co.*, DeVall's Bluff, KU 3806; CM 61728–61740, 61963–61975; UWZM 22022, 22029. *Saline Co.*, Benton, Saline River, USNM 17818–17819, 20958. *Union Co.*, Ouachita River, 12 mi E Strong, TU 16849, 17110. *Yell Co.*, Petit Jean Creek, 10 m W Casa, TU 14566(7), 14568. ILLINOIS: *Calhoun Co.*, Golden Eagle, INHS 7375. *Cass Co.*, Lake Meredosia, CM 107660. *Cumberland Co.*, Greenup, INHS 1964. *DeKalb Co.*, 2 mi W Sandwich, INHS 9326. *Jersey Co.*, Mississippi River, 2 mi N Grafton, UIMNH 1123; 7 mi W Grafton, INHS 1762, 2161–2162. *Madison Co.*, Alton, N side of Mississippi River, FMNH 3464–3465. *Mason Co.*, Havana, SMBU 3104; UIMNH 55; FMNH 95, 475; Illinois River at Havana, FMNH 331. *Massac Co.*, NE edge Leon Lake, UIMNH 56449. *Morgan Co.*, Meredosia, UIMNH 2310; INHS 2131, 2134–2137, 5147–5148. *Pope Co.*, Ohio River, 2 mi S Golconda, CM 107604. *Randolph Co.*, 1 mi W Reilly Lake, INHS 9351. *Shelby Co.*, Shelbyville, INHS 2358. *Wabash Co.*, Mt. Carmel, USNM 10325, 12070, 12795(2), 12795(3). *White Co.*, 9 m SE Crossville, INHS 7170. *Whiteside Co.*, Thompson, CM 107662–107664. INDIANA: *Bartholomew Co.*, E Fork White River at Azalia, CM 65583*, 87546*, 87567*. *Gibson Co.*, Tool Pond, UMMZ 89742. *Knox Co.*, Wheatland, USNM 14669; Vincennes, USNM 22718–22719. *Owen Co.*, 4 mi SW Spencer, UMMZ 111876. *Posey Co.*, 2 mi S New Harmony, INHS 7435–7440. *Vigo Co.*, no specific locality, MCZ 16471. IOWA: *Allamakee Co.*, 1¼–3 mi NNE Lansing, UMMZ 92693, 92695–92696; Mississippi River, 1.2 mi W DeSoto, Wis., UMMZ 92589, 92689–92692. *Clayton Co.*, Clayton, Mississippi River, UMMZ 119504. *Jackson Co.*, no specific locality, UMMZ 86650; Bellevue, UMMZ 72553, 72555. *Lee Co.*, Keokuk, USNM 55259. *Muscatine Co.*, Fairport, USNM 60052–60053. KANSAS: *Cowley Co.*, Winfield, USNM 88800. *Geary Co.*, Republican River, USNM 261. *Montgomery Co.*, Verdigris River, KU 3297–3299. *Woodson Co.*, 2 mi E of Neosho Falls, KU 48251–48257. KENTUCKY: *Trigg Co.*, Sector 6J, Lake Dove, APSU 217(a), 217(b); Sector 8H, APSU 832; 1.6 mi SW 6J4 Lake Shore, APSU 911; S Redd Hollow, APSU 220, 223. LOUISIANA: south central Louisiana, TU 7693. *Bossier Par.*, Curtis, TU 6352. *Bossier/Caddo Par.*, Red River, NLU 9183, 9187, 9368–9373, 20579–20580. *Caddo Par.*, Caddo Lake, TU 7658; Gayle, 1 mi W Red River, CM 4269. *Catahoula Par.*, Ouachita River, 4 mi N Harrisonburg, TU 12535–12536, 12537*, 12545, 12615, 12631, 12651, 12655, 12658, 12664, 12666, 12670, 12695, 12701, 12705, 12707, 12710, 12783, 12968.9, 12975 (paratypes); UMMZ 104320, 104345–104351; 4 mi E Harrisonburg, USNM 139733. *Iberville Par.*, Bayou Pigeon, TU 12131. *Natchitoches Par.*, Vic. of Natchitoches, FWM 3662; Red River at Grande Ecore, CM 62160; 4 mi N Natchitoches, CM 62161. *Orleans Par.*, New Orleans, USNM 69595. *Ouachita Par.*, Monroe, TU 5870, 5872; N Monroe, Monroe Fish Hatchery, CM 39938; NLU 820, 847, 1010–1011, 1122–1125; Ouachita River, Monroe, MAZG 1470; 15 mi SW Monroe, NLU 810–812; Ouachita Bayou, NLU 1517; Ouachita River at Fondale, NLU 31464. *Red River Par.*, Red River at Coushatta, MAZG 1460. *St. Charles Par.*, pond near Mississippi River, USL 1197. *St. Landry Par.*, Bayou Teche in Arnaudville, USL 16373. *St. Martin Par.*, 1 mi S I-10 bridge, Atchafalaya River, USL 22335. MINNESOTA: *Wabasha Co.*, Wabasha, USNM 81992. MISSISSIPPI: *Adams Co.*, Mississippi R., 3 mi S International Paper Co., Natchez, NLU 35939. OHIO: *Franklin Co.*, Columbus, USNM 131884. OKLAHOMA: *Bryan Co.*, Washita Arm of Lake Texoma, UIMNH 20060. *Choctaw Co.*, Red River, opposite Arthur City, Texas, KU 128995. *Comanche Co.*, Ft. Sill, Medicine Creek, AMNH 65522. *Johnston Co.*, FMNH 15469. *Kay Co.*, E Ponca City, UMMZ 89625a–89625b. *Le Flore Co.*, 6.5 mi W Heavener, UOMZ 15708; Poteau Reservoir Stilling Basin, UOMZ 27419. *Marshall Co.*, Lake Texoma, 2 mi E Willis, KU 40168*–40169*, 40170–40171, 40172*, 40173–40174; FWM 3549–3552, 4777–4779, 5457–5459; TU 14503(14), 16661.1, 17300(2); UOMZ 26911–26912, 27129–27130, 27153, 27157, 27175, 27326–27329, 27388, 27551–27554, 27565, 27567–27568, 27573–27576, 27584–27592, 33328–33331. *McCurtain Co.*, no specific locality, UOMZ 2137; 2 mi SW Smithville, UOMZ 17137–17138; Mt. Fork River, Beaver's Bend State Park, FWM 3705; Glover River, 9 mi N Wright City, "Big Rock," CM 61741–61746; Beaver's Bend, TNHC 34020, 34034–34039. TENNESSEE: *Decatur Co.*, near Parsons, TU 14497(4). *Lake Co.*, Mississippi River, 4 mi NW Tiptonville, KU 1769, CM 107736; 3 mi W, 3 mi N Tiptonville, CM 107624, 107641. *Obion Co.*, Reelfoot Lake, UMMZ 99230; KU 88750, 88752–88757. *Perry Co.*, Buffalo River, 3.5 mi N Lobelville, TU 16048; Tennessee River between Saltillo and Dunville, TU 16937(3). TEXAS: *Grayson Co.*, Rocky Pt., Lake Texoma, USNM 20038, UIMNH 20058–20059; "Red River," USNM 69544. WEST VIRGINIA: *Wirt Co.*, Little

Kanawha River, mouth of Reedy Cr., near Palestine, CM 31245-31246, 32063, 35142. WISCONSIN: *Buffalo Co.*, approximately 12 mi above Winona, Minn., Mississippi River, CM 28807. *Columbia Co.*, Wisconsin River, T13NR8W, Sec 32, RCV 73-111-73-112. *Grant Co.*, Millville, Wisconsin River, UWZM 21930; T8NR2W, Sec 1, NE $\frac{1}{4}$ mi, RCV 73-101; T8NR1W, Sec 6, NE $\frac{1}{4}$ mi, RCV 73-102; T6NR6W, Sec 1, RCV 73-119; Mississippi River, 7 mi S Potosi, UMMZ 72508. *Iowa Co.*, Wisconsin River, T8WR2E, Sec 5, RCV 73-103; T8WR3E, Sec 19, RCV 73-104-73-105; T8NR1E, Sec 6, RCV 73-106, 73-108; T8NR3E, Sec 17, RCV 73-107; T8NR3E, Sec 19, RCV 73-109-73-110, 73-120-73-121. *Trempealeau Co.*, Mississippi River, Perrot State Park, T18NR9W, Sec 28, RCV 73-114; Fountain City, CM 107668. *Vernon Co.*, Stoddard, Mississippi River, UWZM 21212, 21296-21316, 21331-21347, 21361-21366, 21378, 21388-21390, 21403-21428, 21431, 21437-21438, 21466-21479, 21510-21515, 21532-21550, 21558-21573, 21583-21587, 21590-21593, 21601-21660, 21666-21678, 21682-21684, 21706-21721, 21732-21735, 21754-21761, 21770-21806, 21817-21856, 21867-21885, 21901-21929, 21931-21939, 21953-21954, 21957, 21959-21960, 21962, 22041-22053, 22055-22062, 22126-22127, 22129-22130, 22133-22139, 22141-22142, 22153-22160, 22179-22180, 22182-22184, 22189, 22192-22194, 22219-22220, 22224-22229, 22241-22252, 22978*, 23000*-23001*, 23009*, 23017*, 23019*-23021*, 23024*, 23029*-23030*, 23038*-23040*, 23044*, 23049*, 23193*-23197*, 23199*-23200*, 23222*-23225*, 23322*-23323*, 23325*-23328*.

Graptemys ouachitensis sabinensis.—LOUISIANA: *Allen Par.*, Calcasieu River, 3 mi W Kinder, TU 15953(1-14); Calcasieu River, 4 mi W Oberlin, TU 3473; Whiskey Chitto Creek between 6 Mile Creek & Hwy 26, USL 23706, 23708. *Beauregard Par.*, Merryville, Sabine River, TU 16840(14); UWZM 22022. *Sabine Par.*, 8 mi SW Negreet, TU 13109-13111, 13116, 13118-13122, 13127-13129, 13131-13150, 13152-13160, 13164, 13166-13175, 13177-13179, 13181-13190, 13192, 13194-13209, 13225-13226, 13510(2), 13760(14); UMMZ 104351-104369; FMNH 73307; USNM 134312; Sabine River at Many, TU 13564(3); TNHC 31359; Sabine River, NLU 1513-1516, 17828; Sabine River Drainage, NLU 28462-28463, 28465-28466. *Vernon Par.*, Sabine River, 1 mi N Toledo Bend Dam, NLU 8139. TEXAS: *Newton Co.*, Bonweir, CM 107771-107773. *Shelby Co.*, Sabine River, Sabine National Forest, E Hamilton Scenic Area, FWM 3565.

Graptemys pseudogeographica pseudogeographica.—ILLINOIS: *Cass Co.*, Meredosia Lake, Honey Pt., CM 107667. *McHenry Co.*, no specific locality, FMNH 2670, 2670a-2670b. *Morgan Co.*, Meredosia, INHS 2130, 2132, 5149-5150. INDIANA: "Grand Chain," MCZ 16486. *Gibson Co.*, Tool Pond, UMMZ 89741, 89743, 92588. *Posey Co.*, 2 mi S New Harmony, INHS 7441-7442. *St. Joseph Co.*, South Bend, Bowman Creek, USNM 194611. *Vigo Co.*, no specific locality, MCZ 16470; Terre Haute, USNM 79. IOWA: *Allamakee Co.*, 6 mi N Lansing, UMMZ 92694. *Des Moines Co.*, Burlington, MCZ 1726. *Jackson Co.*, Bellevue, UMMZ 72552, 72554. *Johnson Co.*, Iowa City, USNM 25394. *Mills Co.*, Mary's Bend, UMMZ 92697-92698. *Muscatine Co.*, no specific locality, TU 1714; $5\frac{1}{2}$ mi SE Muscatine, INHS 7676-7680. KANSAS: *Leavenworth Co.*, Ft. Leavenworth, KU 21532. MINNESOTA: *Brown Co.*, 7 mi W New Ulm, JFBM 1320, 1322, 1354-1355. MISSOURI: *Holt Co.*, no specific locality, KU 88736, 88750. *Lewis Co.*, no specific locality, KU 88735. *Marion Co.*, no specific locality, USNM 19; KU 88747-88748. NEBRASKA: *Boyd Co.*, 5 mi N, 5 mi E Lynch, Missouri River, UN 7117. *Cedar Co.*, 2 mi E St. Helena, SD 2828; Missouri River at Yankton Bridge, UN 6633-6637. *Dakota Co.*, Sioux City, Missouri River, UN 6638. *Dixon Co.*, 1-3 mi W Vermillion (South Dakota), UN 6617-6632. *Richardson Co.*, Missouri River, Falls City, USNM 138872, 153779. *Washington Co.*, $1\frac{1}{2}$ mi E Blair, Missouri River, UN 6639. NORTH DAKOTA: *Sioux Co.*, 4 mi N Ft. Yates, SD 2883. OHIO: "Maumee River," MCZ 1727. *Franklin Co.*, Columbus, USNM 7751. SOUTH DAKOTA: *Bonhomme Co.*, Sand Islands of Charles Creek, SD 1659. *Corson Co.*, ND-SD line, SD 2880, 2882. *Charles Mix Co.*, Platte Creek, SD 2345. *Clay Co.*, 2 mi S Vermillion, SD 41, 2855, 3057-3059. *Gregory Co.*, base of Ft. Randall Dam, SD 2862. *McLean Co.*, $\frac{1}{2}$ mi S Big Bend Dam, SD 2860. *Union Co.*, McCook Lake, SD (Bohan #1); 3 mi SW Elk Pt., SD 12; Missouri River, SD 1534. *Yankton Co.*, below Gavins Pt. Dam, SD 1520. WISCONSIN: *Grant Co.*, Wisconsin River, T6NR5W, Sec 7, SW $\frac{1}{4}$, RCV 73-100; T6NR6W, Sec 1, RCV 73-118. *Polk Co.*, Interstate Park, Lake of the Delles, T34NR19W, Sec 36, RCV 73-117. *Portage Co.*, Wisconsin River, 5 mi W Plover, T25NR7E, Sec 16, RCV 73-113. *St. Croix Co.*, Hudson, UMMZ 72505; St. Croix River, 1 mi N Hudson, JFBM 1089; St. Croix River, 1.2 mi N Somerset, T31NR19W, Sec 7, RCV 73-115-73-116. *Trempealeau Co.*, Fountain City, Mississippi River, CM 107661. *Vernon Co.*, Stoddard, Mississippi River, UWZM 21198-21203, 21317-21330, 21336-21343, 21348-21360, 21367-21377, 21379-21387, 21391-21402, 21415-21417, 21425-21426, 21429-21436, 21439-21465, 21480-21509, 21516-21531, 21551-21557, 21574-21585, 21588-21589, 21594-21600, 21661-21665, 21679-21681, 21685-21686, 21722-21731, 21736-21753, 21761-21770, 21857-21866, 21871-21881, 21886-21900, 21940-21951, 21956, 21961, 22030-22040, 22124-22125, 22128, 22131-22132, 22140, 22143-22146, 22161-22163, 22181, 22185-22188, 22190, 22195-22198, 22221-22223, 22230-22240, 22980*, 22983*-22984*, 22998*, 23002*, 23006*, 23010*-23011*, 23013*-23014*, 23018*, 23021*, 23023*, 23025*-23027*, 23031*-23032*, 23034*-23035*, 23037*, 23041*-23043*, 23047*, 23324*.

Graptemys p. pseudogeographica × *p. kohni*.—ILLINOIS: "Ohio River," UIMNH 2311. *Adams Co.*, Quincy, MCZ 6395; UIMNH 16773; AMNH 4748–4749, 46480. *Cumberland Co.*, no specific locality, FMNH 37931. *Jackson Co.*, Carbondale, SD 3563; Mississippi River, Sand Island, UMMZ 81571–81575. *Obion Co.*, Dyer Co. line, UMMZ 1938. *Madison Co.*, Alton, N side of Mississippi River, FMNH 3463. *Mason Co.*, Havana, UIMNH 53–54, 56–65, 2307; Metropolis, UIMNH 2308. *Monroe Co.*, Mississippi River, INHS 7916–7918. *Pope Co.*, Ohio River, 2 mi S Golconda, CM 107598–107606. *Randolph Co.*, 3 mi NW Chester, INHS 5009. *St. Clair Co.*, USNM 55534. *Wabash Co.*, Mt. Carmel, USNM 12795(1), 12795(4). *White Co.*, 9 mi SE Crossville, INHS 6790. KANSAS: *Douglas Co.*, 5 mi NW LeCompton, Kansas River, KU 40115; 1 mi N, 1½ mi W Lake View, KU 52290. *Geary Co.*, Republican River, USNM 7610; ANSP 260. KENTUCKY: *Ballard Co.*, 3.5 mi N Bandana, Big Turner's Lake, UIMNH 18004. *Fulton Co.*, 4½ mi S Hickman, USNM 104504. *McCracken Co.*, Paducah, USNM 102903. MISSOURI: *Boone Co.*, no specific locality, KU 88738. *Madison Co.*, no specific locality, KU 88746. *Mississippi Co.*, no specific locality, KU 88749. *St. Clair Co.*, no specific locality, USNM 55533–55534. *St. Louis Co.*, no specific locality, USNM 16494, 55529–55531; St. Louis, UIMNH 1660. TENNESSEE: *Henry Co.*, Paris Landing State Park, APSU 853. *Lake Co.*, Reelfoot Lake, UIMNH 2312; CM 107613, 107616–107617; Reelfoot Lake, 2 mi E Markham, UIMNH 1364; 2½ mi SE Tiptonville, UIMNH 1271–1275, 15791; Mississippi River, 3 mi N Tiptonville, CM 107614–107615, 107618–107623, 107625–107659; 4 mi NW Tiptonville, Mississippi River, CM 107669–107754; Edgewater, TU 16239, 17986. *Obion Co.*, Reelfoot Lake, UMMZ 74212–74220, 74612–74615, 84183, 96607; USNM 100471, 100474, 100478, 102924–102925, 102927–102937, 102939–102944, 102946, 103471; TU 19320. *Stewart Co.*, 1.8 mi S 7 PH, APSU 803; 1.2 mi S 7 RS, APSU 811, 812a–812b.

Graptemys pseudogeographica kohni.—ARKANSAS: "Horseshoe Lake," FMNH 194231. *Chicot Co.*, Lake Chicot, CM 107607–107608. *Dallas Co.*, Faringdale, USNM 95369. *Greene Co.*, Paragould, USNM 95382. *Jackson Co.*, Amagon, CM 23997. *Lawrence Co.*, Black River, Powhatan, UMMZ 91386; FMNH 15241–15242, 15248–15249, 92130–92135; Black River, TU 14611*, 15678*. *Monroe Co.*, White River at Clarendon, TU 16886(7). *Prairie Co.*, DeVall's Bluff, White River, KU 1181*, 1871*, 2463*–2464*, 2466*, 2667*–2669*, 2671*, 2679*, 2750*, 2804*, 2808*–2810*, 3107A–3107B, 3108, 3110–3112, 3232–3240, 3254, 3340–3341, 3343, 3344A–3344B, 3345, 3356, 3360, 3371, 3373–3413, 3416–3425, 3780, 3791, 3795–3798, 3800–3805, 3807–3826; CM 60401, 61708–61713, 61715–61725; UWZM 22008. *Pulaski Co.*, Lake 5 mi E North Little Rock, CM 24616–24620, 25148. *St. Francis Co.*, 5.5 mi W Forrest City, U.S. 70, CM 25067, 25072. *Union Co.*, Ouachita River, 12 mi E Strong, TU 16843(6). *Yell Co.*, Petit Jean Creek, 10 mi W Carson, TU 14567(17). KANSAS: *Coffey Co.*, Neosho River, KU 3287–3288. *Osage Co.*, Lang Creek, KU 3164. *Wilson Co.*, 1 mi S Altoona, Verdigris River, KU 3257, 46746. LOUISIANA: "South Central Mississippi Valley," TU 1348(60), 6318. *Acadia Par.*, Rayne, USL 324-3. *Bossier/Caddo Par.*, Red River, 11 mi N Bossier City, NEI 9185. *Caddo Par.*, Caddo Lake, TU 405, 416, 491–494, 496–498, 500, 635–636, 643–645(2), 684–687, 698–699, 1240, 5014, 7603–7604, 7607, 7610, 7616, 7629, 7656, 7667, 7675, 7691; Gayle, 1 mi W Red River, CM 4252–4268, 4270–4271; FMNH 8010. *Catahoula Par.*, Jonesville, TU 7533(7); Wells Lake, N Jonesville, NLU 1634; Ouachita River, 4 mi W Harrisonburg, TU 12538, 12541, 12543, 12627, 12630, 12632, 12635–12636, 12641, 12647, 12653, 12659–12660, 12662–12663, 12668, 12673–12674, 12685, 12689–12690, 12692–12694, 12698–12700, 12748, 12782, 12784, 12786, 12975, 13001, 13527(3), 16894. *Claiborne Par.*, Corney Lake, Summerfield, TU 1366. *Concordia Par.*, Deer Park, CM 107611–107612; Shaw, TU 7080, 7118, 7121, 7125, 7148, 7151, 7156–7158, 7163–7164, 7187, 7201, 7204–7205, 7218, 7222, 7235, 7246–7247, 7259, 7266, 7268–7269, 16063(22); 1–4 mi N Natchez (MS), Mississippi River, NEI 8905–8907, 8912; Riflepoint, near Natchez (MS), UMMZ 76488; Red River, Shaw, USNM 99887–99890. *DeSoto Par.*, Wallace Bayou, SMBU 2367–2368, 2372, 2376–2378, 2380–2383, 2387–2389, 2438–2441, 7753, 7760, 7767. *Franklin Par.*, Bayou Pigeon, TU 11874; Wisner, TU 7541(5), 7564(2); Turkey Cr., Winnsboro, NLU 1625–1626. *Iberville Par.*, no specific locality, TU 12121*, 16324*; Mississippi River, 2 mi N Plaquemine, CM 62151; Plaquemine, USNM 100242–100250, 100254, 100258–100263, 100265–100274, 100276–100283, 100475, 100477–100479. *Lafayette Par.*, Bayou Pkwy., USL 10640. *LaFourche Par.*, Thibodaux, CM 7518. *Morehouse Par.*, Horseshoe Lake at Oak Ridge, NLU 29172–29191. *Natchitoches Par.*, Bayou SW Natchitoches off Cane River, UIMNH 91076; Natchitoches, CM 62153; Red River at Grand Ecore, CM 62160; 4 mi W of Natchitoches, CM 62161; Cane River, CM 62152. *Orleans Par.*, New Orleans, TU 17252. *Ouachita Par.*, Monroe, TU 5869, 5871; Bayou DeSiard at Hwy 165, CM 44427–44429; 15 mi S Monroe, CM 39949; Bayou DeSiard at Webster St., CM 39950, 39951a–39951h; Bayou DeSiard at Monroe, MAZG 1456–1457, 1462, 1469; Ouachita River, 15 mi SE Monroe, MAZG 1465; Wall Lake, 9 mi E Monroe, MAZG 1455, 1458, 1463, 1466; Bayou DeSiard, NEI 8424; NLU 4971–4979; Moon Lake, Ouachita River oxbow, 3 mi W Monroe, NLU 8255; 4.8 mi N Monroe on Hwy 165, NLU 21352–21355; Monroe Fish Hatchery, NLU 4964–4965, 4986; LWFC office, W Monroe on US 65, NLU 21668; Hwy 553, 5.5 mi W of Hwy 165, NLU 22503; Hwy 553 between

Hwy 153 & Hwy 134, NLU 23263. *Pointe Coupee Par.*, False River, New Roads, USNM 100217–100219. *Richland Par.*, Kayville, USNM 100472, 100476; Brown Minnow Farm, NLU 1663; Bayou Fisheries at Archibald, NLU 4131, 4169. *Sabine Par.*, 8 mi NW Negreet, TU 13112–13114, 13117, 13123–13126, 13136, 13138, 13151, 13165, 13176, 13180, 13191, 13193, 13742(14), 13760(8). *St. Charles Par.*, no specific locality, TU 10237*. *St. James Par.*, Vacherie, TU 10235, 12074–12075. *St. Landry Par.*, Bayou Courtableau, USL 24027, 24030–24032; Courtableau Bayou, 11 mi N Butte LaRose, Exit I-10, USL 23557; Bayou Teche in Arnaudville, USL 16320–16321, 16332, 19222–19226; 2 mi W Krotz Springs, USL (uncatalogued); 3.5 mi N Three Mile Lake, USL 23296. *St. Martin Par.*, 8 mi E Henderson along Butte LaRose Canal, NLU 29541; Henderson Swamp, USL 7113; Henderson Lake, Butte LaRose Canal, USL 14171, 14382–14383, 22518; 7.1 mi S Henderson, USL 21156; 1 mi W Butte LaRose, USL 22273; Little Alabama Bayou, USL 24109–24110. *St. Mary Par.*, Morgan City, UMMZ 76447. *Tangipahoa Par.*, Ponchatoula, FMNH 22897. *Tensas Par.*, Tensas River, TU 11877, 11901(8). *Union Par.*, Ouachita River, USNM 138945; D'Arbonne Bayou, below Dam, NLU 7726–7728, 7736, 7747, 7749–7755, 17287; NEI 7728; Camp Creek at Hwy 15, NLU 20858; Bayou Bartholomew, TU 12844, 12847–12851, 12868(6), 12968(16), 13039. *Webster Par.*, Minden, AMNH 42330–42332. MISSISSIPPI: *Adams Co.*, Washington, MCZ 1728–1729; Natchez, MCZ 1730–1732, 46560. *Bolivar Co.*, Deeson, TU 19312–19315. *Humphrey Co.*, Wasp Lake, Belzoni, USNM 102704. *LeFlore Co.*, Greenwood, USNM 73670–73672. *Sunflower Co.*, Indianola, Lake Macon, USNM 102702; Shakelford, USNM 102703. *Washington Co.*, Lake Washington, UMMZ 77705, 77706a–77706f; Leroy Percy State Park, CM 107609–107610. *Yazoo Co.*, Panther Creek, W Yazoo City, UMMZ 86666–86667, 86671–86673; Yazoo River, USNM 95136–95137. *Yazoo/Madison Co.*, Big Black River on Hwy 29, TU 14581(10). MISSOURI: *McDonald Co.*, no specific locality, KU 88745. OKLAHOMA: *Cherokee Co.*, no specific locality, TU 13866*; Illinois River, between Hanging Rock and Echota Access Area, CM 61726–61727. *Le Flore Co.*, Wister, CM R3062; 6 mi S Wister, UOMZ 1638, 2138, 2540k; 1.5 mi E Zoe, UOMZ 15853, 16800. *McCurtain Co.*, Glover River, 9 mi N Wright City, “Big Rock,” CM 61714, 61962; UOMZ 2139, 2142; Beaver's Bend State Park, UOMZ 29290; TNHC 34021. *Okmulgee Co.*, no specific locality, UOMZ 12415. TEXAS: “Red River,” USNM 69545. *Anderson Co.*, Trinity River, USNM 17692–17695. *Brazos Co.*, Wickson Lake, TCWC 688, 690. *Cass Co.*, 5.6 mi E Linden, SMBU 16297. *Grayson Co.*, Lake Texoma, TCWC 7270. *Grimes Co.*, Navasota River, 2 mi SE Junction, FMNH 1179, 2038; TCWC 21412; Navasota River at Sulphur Springs, TCWC 23538; Navasota, 16 mi SE College Station, UIMNH 20199. *Hardin Co.*, 2 mi NE Saratoga, UIMNH 1276. *Harrison Co.*, Lake Caddo, AMNH 16967, 16984. *Henderson Co.*, Chandler, USNM 95401. *Lamar Co.*, Arthur, FMNH 460a–460c. *Leon Co.*, Clear Lake, 16 mi S Oakwood, SMBU 6694–6696. *Liberty Co.*, Big Creek near junction with Trinity River, TU 14370, 14393, 14400. *Madison Co.*, Twin Lakes, TCWC 519–520. *Newton Co.*, Bonweir, EOM 1853. *Orange Co.*, 10 mi N Orange, SMBU 13248. *Robertson Co.*, Oak Creek, Hwy 66, 3.4 mi N Ridge, TCWC 689, 30784–30785. *Shackelford Co.*, Clear Fork Brazos River, Ft. Griffin State Park, TU 14544*. *Shelby Co.*, Sabine River, 31.7 mi NW Joaquin, TU 14357. *Walker Co.*, 14.1 mi W Huntsville, TU 14354.

Graptemys versa.—TEXAS: “Colorado River,” TU 14484.3*, 16190*. *Burnet Co.*, Morgan Creek, SMBU 7814. *Coleman Co.*, 20 mi S Valera, SMBU 10609–10619. *Edwards Co.*, 3 mi SW 700 Springs, FMNH 92145. *Kimble Co.*, S Llano River, SW Junction, SMBU 2112; 3 mi SE Telegraph at Paint Rock Ranch, SMBU 5074–5099, 5101–5102. *McCulloch Co.*, 3 mi SW Leaday, SMBU 3344, 5103–5104, 5106–5115, 5700. *Menard Co.*, San Saba River, 3 mi E Menard, SMBU 89410. *San Saba Co.*, 6 mi W Beaver, Royal Creek, FMNH 55556–55557, 55561; Rough Creek, 7.5 mi SE San Saba, FWM 2642; 4 mi NW Bend, FWM 3564; 11 mi NW Bend, FWM 5477; 5 mi SW Algerita, FWM 6909. *Travis Co.*, Austin, MCZ 42346; USNM 27473–27479.

NEW SPECIES AND RECORDS OF CADDISFLIES
(INSECTA: TRICHOPTERA) FROM THE LESSER ANTILLES,
WITH SPECIAL REFERENCE TO GRENADA

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ABSTRACT

Twenty-two species of caddisflies are now known from the island of Grenada. Of these, *Xiphocentron* (*Antillotrichia*) *lobiferum*, n. sp., *Bredinia* *appendiculata*, n. sp., *Neotrichia* *nesiotes*, n. sp., *Amphoropsyche* *woodruffi*, n. sp., and *Helicopsyche* *grenadensis*, n. sp. are described herein. Additional records and descriptions are given for other species from the islands of Guadeloupe, Dominica, St. Lucia, and St. Vincent. *Chimarra* *diannae*, n. sp., is described from St. Lucia and *Ochrotrichia* (*M.*) *rawlini*, n. sp., from Dominica. A list of all the species known from the Lesser Antilles is given.

INTRODUCTION

The first caddisfly recorded from the Lesser Antilles was *Leptonema albovirens* from St. Vincent (Mosely, 1933), a species that is widespread in central and northern South America. The second species, *Polycentropus insularis* (Banks, 1938), was described from Grenada shortly thereafter. The islands were then ignored until 1968 when Flint reported on major collections made on Dominica, St. Lucia, and Grenada. Flint's study and other published records raised the number of known species to 36 on Dominica, 11 on St. Lucia, 12 on Grenada, three on Guadeloupe and one on St. Vincent. The next major thrusts were several primarily limnological investigations, the first by Harrison and Rankin on St. Vincent (1976), the second by Starmuhlner and Therezien primarily on Guadeloupe with stops on Dominica and Martinique. The Trichoptera collected by this latter expedition were studied by Malicky (1980, 1983, 1987), and brought the species total known from Guadeloupe to 21 and added the first three for Martinique. Botosaneanu made expeditions to Martinique in 1986, and to Curaçao, St. Vincent, Martinique, and Barbados in 1989, resulting in a series of papers (1988, 1989, 1990a, 1990b) which greatly increased knowledge of caddisflies from these islands. Recent collections from Grenada, St. Vincent, St. Lucia, Dominica, and Guadeloupe, listed below, are reported herein.

R. E. Woodruff, Florida Department of Agriculture, led a major expedition to Grenada in 1990 resulting in 36 samples of Trichoptera. A blacklight trap was the method most often used to make these collections, but a few malaise trap samples were also obtained. Most of the material was obtained from a permanent site located at the Agricultural Laboratory at Mirabeau, Parish St. Andrews. This collection is deposited primarily in the Florida State Collection of Arthropods (FSCA), with specimens at the Carnegie Museum of Natural History (CMNH) and the National Museum of Natural History (NMNH).

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An expedition by J. E. Rawlins and S. A. Thompson from the Carnegie Museum of Natural History in 1991 resulted in small but valuable collections of Trichoptera from St. Lucia and Dominica. Among these were a new species of *Ochrotrichia* (*Metrichia*) from Dominica and a new *Helicopsyche* record from St. Lucia. This material is deposited at the Carnegie Museum.

Two other small collections, preserved at the National Museum of Natural History, are also reported upon in this paper. One from Grand Etang, Grenada, made by E. L. Todd, Systematic Entomology Laboratory, U.S. Department of Agriculture, produced the first record of the genus *Oecetis* from the island. On the same trip Todd and C. L. de Freitas collected on St. Vincent. Most of the species they took on that island were reported by Botosaneanu (1990a), and one more species record is added herein. The second collection was made on St. Lucia and Dominica by W. N. Mathis, Department of Entomology, National Museum of Natural History.

The accompanying table summarizes the results of this collecting activity. Between Guadeloupe and Grenada, a total of 65 species have now been identified. An identification to generic level, usually based on females or larvae, is counted as one species for a particular island until the first species record is made (unless the record was clearly for a second species from the island), at which point the generic record is dropped. The list of species known from Grenada is increased from 12 to 22, which compares well to the numbers known on other Lesser Antillean islands: Guadeloupe, 22; Dominica, 37; Martinique, 20; St. Lucia, 13; St. Vincent, 15; Barbados, 2; Mustique, 1 (Table 1). However, a number of genera that are widely distributed in the Lesser Antilles are still unknown from Grenada, and their inevitable discovery will further increase the number. Some genera noticeably absent are: *Cernotina*, *Alisotrichia*, and *Ochrotrichia* (*Metrichia*). Other genera, such as *Protoptila*, *Austrotinodes*, *Atanatolica*, and *Phylloicus*, are known only from a single or a few islands and may not exist on all islands. Most of these genera have adults active in daytime that rarely appear in light trap collections, which probably accounts for their sporadic records.

SYSTEMATICS

Wormaldia planae Ross and King

Described originally from Mexico, this species has been reported from Guatemala, Panama, Columbia, Venezuela, Brazil, Ecuador, Trinidad, Tobago, and Grenada (two miles west of Grand Etang) (Flint, 1968, 1991). On the basis of these collections, *W. planae* is infrequently encountered on the island of Grenada.

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Laboratory, 1 Feb. 1990, A. Thomas, 1 male; same, 23 Feb. 1990, R. E. Woodruff, 1 male; same, 12 Oct. 1990, 1 male; road end at Mt. St. Catherine, 22 Feb. 1990, R. E. Woodruff, et al., 5 males and 3 females; PARISH ST. JOHNS: Concord Falls, 20 Feb. 1990, R. E. Woodruff, et al., 4 males and 5 females (all FSCA).

Chimarra diannae, new species

Fig. 1–3

Diagnosis.—This species is similar to *C. dominicana* but differs in the structure of the male genitalia, especially the tenth tergites and claspers. In *C. dominicana* the dorsal branch of the tenth tergum is short, tapered and straight, whereas in *C. diannae* it is proportionately longer, terete, and arched. The ventral branch of the tenth tergum in *C. dominicana* bears two strong, laterally directed teeth at its

Table 1.—Distribution of the Trichoptera recorded from the Lesser Antilles. (GU = Guadeloupe, DO = Dominica, MA = Martinique, SL = St. Lucia, SV = St. Vincent, MU = Mustique, GR = Grenada, BA = Barbados)

	GU	DO	MA	SL	SV	MU	GR	BA
<i>Protoptila dominicensis</i>	X							
<i>Wormaldia planae</i>					X		X	
<i>Chimarra dominicana</i>	X	X	X					
<i>Chimarra diannae</i>				X				
<i>Chimarra antillina</i>	X	X	X	X				
<i>Chimarra caribea</i>							X	
<i>Chimarra hairouna</i>					X			
<i>Xiphocentron fuscum</i>		X		?				
<i>Xiphocentron parentum</i>			X					
<i>Xiphocentron albolineatum</i>		X			X			
<i>Xiphocentron lobiferum</i>							X	
<i>Austrotinodes madininae</i>			X					
<i>Cernotina lutea</i>		X						
<i>Cernotina cadeti</i>				X				
<i>Cernotina</i> sp.	X							
<i>Polyplectropus bredini</i>	X	X	X	X			X	
<i>Polycentropus insularis</i>		X					X	
<i>Smicridea cariba</i>		X						
<i>Smicridea simmonsii</i>			X	X	X			
<i>Smicridea grenadensis</i>							X	
<i>Smicridea astarte</i>	X							
<i>Smicridea palifera</i>							X	
<i>Smicridea</i> sp.					X			
<i>Leptonema archboldi</i>		X	X					
<i>Leptonema albovirens</i>					X		X	
<i>Leucotrichia sarita</i>							X	
<i>Leucotrichia</i> sp.			X					
<i>Zumatrichia antillensis</i>	X	X	X	X	X		X	
<i>Zumatrichia anomaloptera</i>	X	X	X	X	X		X	
<i>Zumatrichia lezarda</i>	X							
<i>Alisotrichia orophila</i>		X	X					
<i>Alisotrichia timouchela</i>			X		X			
<i>Alisotrichia lobata</i>		X						
<i>Alisotrichia dominicensis</i>		X	X					
<i>Brysopteryx septempunctata</i>		X						
<i>Neotrichia iridescens</i>	X	X	X	X				
<i>Neotrichia corniculans</i>		X						
<i>Neotrichia tauricornis</i>	X		X	X			X	
<i>Neotrichia nesiotis</i>							X	
<i>Neotrichia pequenita</i>								X
<i>Neotrichia</i> sp.					X			
<i>Bredinia dominicensis</i>		X						
<i>Bredinia appendiculata</i>							X	
<i>Oxyethira janella</i>	X	X	X	X	X		X	X
<i>Oxyethira azteca</i>							X	
<i>Oxyethira arizonensis</i>		X	X					
<i>Oxyethira tega</i>	X	X						

Table 1.—Continued.

	GU	DO	MA	SL	SV	MU	GR	BA
<i>Hydroptila martorelli</i>	X							
<i>Hydroptila antillarum</i>	X	X	X	X				
<i>Hydroptila grenadensis</i>							X	
<i>Hydroptila</i> sp.					X			
<i>Ochrotrichia</i> (O.) <i>brayi</i>		X						
<i>Ochrotrichia</i> (O.) <i>ponta</i>		X	X		X		X	
<i>Ochrotrichia</i> (O.) <i>spinosissima</i>		X						
<i>Ochrotrichia</i> (O.) sp.	X							
<i>Ochrotrichia</i> (M.) <i>campana</i>		X						
<i>Ochrotrichia</i> (M.) <i>similis</i>	X	X						
<i>Ochrotrichia</i> (M.) <i>exclamationis</i>		X						
<i>Ochrotrichia</i> (M.) <i>rawlinsi</i>		X						
<i>Oecetis pratti</i>		X					X	
<i>Oecetis knutsoni</i>	X							
<i>Atanatolica dominicana</i>	X	X						
<i>Atanatolica</i> sp.					X			
<i>Amphoropsyche insularis</i>	X	X						
<i>Amphoropsyche janstockiana</i>					X			
<i>Amphoropsyche woodruffi</i>							X	
<i>Amphoropsyche</i> sp.						X		
<i>Phylloicus monticolus</i>		X						
<i>Phylloicus</i> sp.	X							
<i>Helicopsyche apicauda</i>		X						
<i>Helicopsyche guadeloupensis</i>	X	X	X	X				
<i>Helicopsyche margaritensis</i>							X	
<i>Helicopsyche grenadensis</i>							X	
Totals	22	37	20	13	15	1	22	2

apex, which are absent in *C. diannae*. The spine at the tip of the clasper in *C. dominicana* is very long and slender, almost hairlike, whereas in *C. diannae* it is short and toothlike.

Description.—Male: Length of forewing, 4 mm. Color fuscous. Forewing lacking bulla in radial system; hindwing with three branches to Rs and two to M. Male genitalia: Eighth segment with sternum narrow, tergum broader dorsally with dorsolateral angles developed into short, sharp points. Ninth segment with anterior margin slightly widened laterally, posterior margin vertical, dorsum developed into a flat lobe over base of tenth tergum; posteroventral process short, thumblike. Cercus thin, twisted dorsolaterad, in posterior aspect large, ovate. Tenth tergum divided into distinct dorsal and ventral branches: dorsal branches widely separated mesally, nearly as long as ventral branch, curved dorsally in lateral aspect, terete, slightly enlarged at apex and with several sensillae; ventral branches platelike, united basally, heavily sclerotized ventrally and apically. Clasper elongate, slender, curved mesad apically; apex with a darkened projection directed dorsomesad, about as long as broad basally in dorsal aspect. Phallus inflated basally (portion now lost); internally with a basal ring attached to an elongate sclerite widened apicad, two elongate spines much enlarged basad, and a pair of small, dark spines apicoventrally at tip.

Type specimen.—Holotype, male (NMNH): ST. LUCIA, QUARTER OF SOUFRIERE, Fond St. Jacques (13°50'N, 61°02'W), 13–14 June 1991, W. N. and D. Mathis.

Etymology.—Named in honor of Mrs. Dianne Mathis, co-collector of this new species.

Remarks.—This is the sister species of *C. dominicana*, which was originally



Fig. 1–3.—*Chimarra diannae*, n. sp., male genitalia: 1, left lateral view; 2, phallus, left lateral view; 3, dorsal view.

described from higher elevations on Dominica, but since has been recorded from Guadeloupe and Martinique (Botosaneanu, 1988, 1990a; Malicky, 1983).

Chimarra caribea Flint

This species, which is similar to *C. duckworthi* Flint, was reported and described by Flint (1968) from Grenada. The holotype was collected two miles west of Grand Etang. Based on the present collections, *C. caribea* is a frequently collected caddisfly in Grenada.

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agriculture Laboratory, 28 Jan. 1990, J. Telesford, 3 males and 2 females; same, 29 Jan. 1990, A. Thomas, J. Telesford, 2 males and 2 females; same, 31 Jan. 1990, M. Thomas, 4 males; same, 1 Feb. 1990, A. Thomas, 2 males; same, 19 Feb. 1990, R. E. Woodruff, 4 males and 5 females; same, 21 Feb. 1990, R. E. Woodruff, 6 males, 2 females; same, 22 Feb. 1990, R. E. Woodruff, 3 males and 4 females; same, 23 Feb. 1990, R. E. Woodruff, 1 male and 2 females; same, 24 Feb. 1990, R. E. Woodruff, 3 males and 1 female; same, 4 March 1990, B. Williams, 1 female; same, 6 March 1990, H. Thomas, 1 male and 3 females; same, 13 March 1990, J. Telesford, 2 males and 1 female; same, 15 May 1990, A. Thomas, 4 males and 1 female; same, 8 June 1990, J. Telesford, 3 males; same, 27 Sept. 1990, R. E. Woodruff, 1 male; same, 12 Oct. 1990, R. E. Woodruff, 1 female; Balthazar Estate, 12 June 1990, J. H. Frank, A. Thomas, 4 females; Balthazar River, Dennis Noel Farm, ca. 3 mi SW Grenville, 25 Feb. 1990, R. E. Woodruff, 1 male and 1 female; road end at Mt. St. Catherine, 22 Feb. 1990, R. E. Woodruff et al., 1 female; Windsor Estate, 6 March 1990, R. E. Woodruff et al., 1 female; Lake Grand Etang, TV Tower, 580 meter elevation, 26 Sept. 1990, R. E. Woodruff et al., 2 males and 2 females; Clabony, 12 Oct. 1990, R. E. Woodruff, A. Thomas, 1 male and 3 females. PARISH ST. JOHNS: Concord Falls, 20 Feb. 1990, R. E. Woodruff et al., 17 males and 36 females; Black Bay, 26 Feb. 1990, R. E. Woodruff et al., 1 male; Clozier, 27 Sept. 1990, R. E. Woodruff et al., 3 males and 6 females. PARISH ST. MARKS: Diamond Estate, 9 Oct. 1990, R. E. Woodruff et al., 1 female (all in FSCA).

Xiphocentron (Antillotrichia) fuscum Flint

This species, which was originally described by Flint (1968) from several sites around Pont Casse, Dominica, has not been recorded since. Another male has recently been collected by W. N. and D. Mathis from the same area. A female was also taken on St. Lucia, where only larvae were recorded previously (Flint, 1968). In size and color it is in complete agreement with the Dominican *X. fuscum*, to which it is provisionally referred.

Material.—DOMINICA, PARISH ST. PAUL, Pont Casse (15°22'N, 61°21'W), 18 June 1991, W.

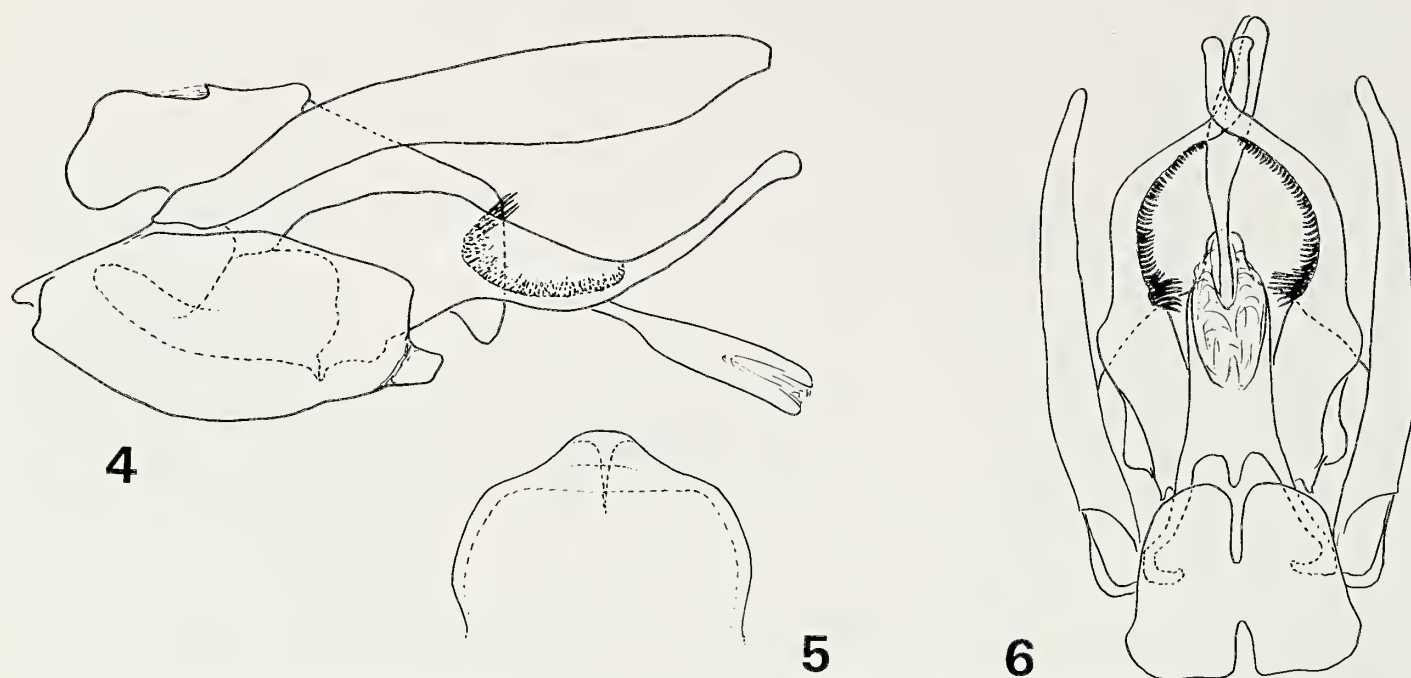


Fig. 4–6.—*Xiphocentron* (*Antillotrichia*) *lobiferum*, n. sp., male genitalia: 4, left lateral view; 5, posterior margin of ninth sternum, ventral view; 6, dorsal view.

N., D. Mathis, 1 male. ST. LUCIA, QUARTER OF SOUFRIERE, Fond St. Jacques (13°50'N, 61°02'W), 13–14 June 1991, W. N. and D. Mathis, 1 female (all in NMNH).

Xiphocentron (*Antillotrichia*) *lobiferum*, new species

Fig. 4–6

Diagnosis.—Distinguished by the shape of ninth sternum with posterior margin bearing a knob-like projection and by the posterior and anterior margins of ninth tergum with deep mesal incisions.

Description.—Male: Length of forewing, 3.5 mm. Color in alcohol fuscous, immaculate. Apical spur of hindleg almost $\frac{1}{2}$ length of basal tarsal segment. Fifth sternum with anterior margin modified, glandular, with dorsal angle produced into an erect process $\frac{2}{3}$ length of sternum. Male genitalia: Ninth sternum with anterolateral process short, rounded, posterior margin produced mesally into a knob-like lobe in lateral aspect; tergum with anterior margin divided mesally by a deep excision, posterior margin similarly divided by an even deeper excision, lateral lobes broad, rounded laterad. Cercus almost perfectly straight, slightly widened subapically, about seven times as long as wide in lateral aspect. Tenth tergum elongate, tip decurved, sclerotized dorsomesally. Clasper long, tip curved dorsally and mesally, terete, broader basally with inner surface bearing many short, dark setae, with a larger cluster of these setae at base of row. Phallus with a very long, slender, tubular basal portion, apex slightly inflated, divided on one side.

Type specimen.—Holotype, male (FSCA); GRENADA, PARISH ST. PATRICK: Plains, 7 April 1990, A. Thomas (malaise trap).

Etymology.—Latin: “bearing lobes,” referring to the distinctive ninth sternum.

Remarks.—This species is closely related to *X. parentum* Botosaneanu and *X. fuscum* Flint. When the male genitalia of all three species are compared side by side, many differences become apparent, which may not be clear in published illustrations. The fifth sternum of all three bears a glandular development along the anterior margin, ending in a projection at the dorsal angle. In *X. fuscum* and *X. lobiferum* this projection is erect and about $\frac{2}{3}$ as long as the length of the segment, but in *X. parentum* it is a very small knob hardly as high as long. The posterior margin of the ninth sternum of *X. lobiferum* bears a distinct mesal

projection, whereas in the other two species it is perfectly straight. The ninth tergum is different in all three species: in lateral aspect the anterior margin is square in *X. fuscum*, in the other two the ventral angle is rounded and produced ventrad. In dorsal aspect the posterior margin is deeply divided mesally with broad lateral lobes in *X. lobiferum*, in the other two it is shallowly notched mesally and the lateral lobes differently shaped. The anterior margin is also different: deeply divided in *X. lobiferum*, straight in *X. fuscum*, and slightly notched in *X. parentum*.

Xiphocentron (Antillotrichia) albolineatum Flint

This is the first record of this species outside Dominica, its type locality.

Material.—ST. VINCENT, PARISH ST. PATRICK, Belleisle, 12 Nov. 1975, E. L. Todd, 1 male (NMNH).

Polycentropus insularis Banks

Originally described from Grand Etang, Grenada, this species also has been recorded from Dominica (Flint, 1968). This record is the first collection from Grenada since the type collection in 1910; interestingly, both are from the same site.

Material.—GRENADA, PARISH ST. ANDREWS: Grand Etang, 23 Oct.–1 Nov. 1975, E. L. Todd, 3 females (NMNH).

Smicridea grenadensis Flint

This species is known only from Grenada. The holotype was collected near Grand Etang.

Material.—GRENADA, PARISH ST. ANDREWS: Clabony, 12 Oct. 1990, R. E. Woodruff, A. Thomas, 1 male and 1 female. PARISH ST. JOHNS: Concord Falls, 20 Feb. 1990, R. E. Woodruff et al., 2 males and 2 females (all in FSCA).

Smicridea palifera Flint

This is a new record for the Island of Grenada. The species was previously known from a number of localities in Venezuela.

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Station, 28 Jan. 1990, J. Telesford, 1 male; Pearls Airport Area, 460 meters behind beach, 8 March 1990, R. E. Woodruff et al., 4 males (all in FSCA).

Smicridea (S.) simmonsii Flint

The identity of this species, originally described from St. Lucia, was recently clarified by Botosaneanu (1990a). It is now also known from Martinique and St. Vincent. The acquisition of three specimens, pinned in the field, allows us to describe the appearance of the species from the type-locality island. The basic color is fuscous, with creamy-white markings. The hair on the front and dorsum of the head and mesally on the mesonotum is pale. The forewings have a broad and somewhat diffuse transverse band from the stigma most of the way across the wing, and a diffuse longitudinal band over the anal cells. The legs, except for the hind tibiae and tarsi which are fuscous, are stramineous. This coloration is basically the same as that described by Flint and Denning (1989) for specimens from St. Vincent (under the name *Smicridea aurimacula*). The overall effect, however, is quite different. The St. Lucian examples are darker and faintly marked

with cream-colored hair, whereas the marking of the St. Vincent material is much more intensely golden and nearly covers the forewing leaving only a small dark mark centrally. In spite of this, the basic pattern is the same, differing only in degree of development. The male genitalia are the same.

Material.—ST. LUCIA, QUARTER OF SOUFRIERE, Fond St. Jacques (13°50'N, 61°02'W), 13–14 June 1991, W. N. and D. Mathis, 3 males (NMNH).

Leptonema albovirens (Walker)

This is a very common species ranging from the USA (Texas) and Mexico across Central America, Columbia, and Venezuela and up the Lesser Antilles at least as far as St. Vincent (Flint et al., 1987). It was reported from Grenada by Flint (1968).

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Laboratory, 28 Jan. 1990, J. Telesford, 6 females; same, 29 Jan. 1990, A. Thomas, J. Telesford, 4 males and 12 females; same, 31 Jan. 1990, M. Thomas, J. Telesford, 1 male and 3 females; same, 1 Feb. 1990, A. Thomas, 1 male and 7 females; same, 19 Feb. 1990, R. E. Woodruff, 2 females; same, 21 Feb. 1990, R. E. Woodruff, 1 male and 1 female; same, 22 Feb. 1990, R. E. Woodruff, 2 females; same, 23 Feb. 1990, R. E. Woodruff, 1 female; same, 6 March 1990, A. Thomas, 2 males and 7 females; same, 13 March 1990, J. Telesford, 1 female; same, 8 June 1990, J. Telesford, 1 male and 3 females; same, 27 Sept. 1990, R. E. Woodruff, 3 females; same, 12 Oct. 1990, R. E. Woodruff, 1 male and 3 females; Balthazar Estate, 1 June 1990, J. H. Frank, A. Thomas, 2 males and 13 females; same, 12 June 1990, 1 male and 1 female; same, 27 Sept. 1990, R. E. Woodruff, 3 females; Windsor Estate, 6 March 1990, R. E. Woodruff, et al., 2 females; Pearls Airport Area, 500 yds behind beach, 8 March 1990, R. E. Woodruff, et al., 2 females; Lake Grand Etang, TV Tower, 580 meters elevation, 26 Sept. 1990, R. E. Woodruff et al., 5 females; Clabony, 12 Oct. 1990, R. E. Woodruff, A. Thomas, 5 males and 9 females. PARISH ST. JOHNS: Black Bay, 26 Feb. 1990, R. E. Woodruff et al., 1 female; Clozier, 27 Sept. 1990, R. E. Woodruff et al., 1 female. PARISH ST. DAVID: Crocha Estate, 5 Oct. 1990, R. E. Woodruff et al., 1 male and 1 female. PARISH ST. MARKS: Diamond Estate, 9 Oct. 1990, R. E. Woodruff et al., 1 female (all in FSCA); Grand Etang, 23 Oct.–1 Nov. 1975, E. L. Todd, 1 male and 8 females (NMNH).

Leucotrichia sarita Ross

This is a widely distributed species which ranges from Texas to Costa Rica. It was reported from Grenada by Flint (1968).

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Laboratory, 8 June 1990, J. Telesford, 1 male; Balthazar River, Dennis Noel Farm, ca. 3 mi. SW Grenville, 25 Feb. 1990, R. E. Woodruff, 1 male; Windsor Estate, 6 March 1990, R. E. Woodruff et al., 1 male. PARISH ST. JOHNS: Black Bay, 26 Feb. 1990, R. E. Woodruff et al., 1 male (all in FSCA).

Zumatrichia antilliensis Flint

This species is captured very commonly in light traps on Grenada. Only males were identified and counted.

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Laboratory, 28 Jan. 1990, J. Telesford, 4 males; same, 29 Jan. 1990, A. Thomas, J. Telesford, 2 males; same, 31 Jan. 1990, M. Thomas, J. Telesford, 3 males; same, 1 Feb. 1990, A. Thomas, 3 males; same, 19 Feb. 1990, R. E. Woodruff, 10 males; same, 23 Feb. 1990, R. E. Woodruff, 6 males; same, 24 Feb. 1990, R. E. Woodruff, 4 males; same, 4 March 1990, B. Williams, 6 males; same, 6 March 1990, A. Thomas, 21 males; same, 13 March 1990, 8 males; same, 15 May 1990, A. Thomas, 6 males; same, 8 June 1990, 13 males; same, 27 Sept. 1990, R. E. Woodruff, 4 males; same, 3 Oct. 1990, R. E. Woodruff, 2 males; Balthazar Estate, 1 June 1990, J. H. Frank, A. Thomas, 47 males; same, 12 June 1990, 11 males; Balthazar River, Dennis Noel Farm, ca. 3 mi SW Grenville, 25 Feb. 1990, R. E. Woodruff, 3 males; Windsor Estate, 6 March 1990, R. E. Woodruff et al., 16 males. PARISH ST. JOHNS: Clozier, 27 Sept. 1990, R. E. Woodruff et al., 1 male; Grenville Vale, 3 Oct. 1990, R. E. Woodruff et al., 1 male; Black Bay, 26 Feb. 1990, R. E. Woodruff et al., 3 males (all in FSCA).

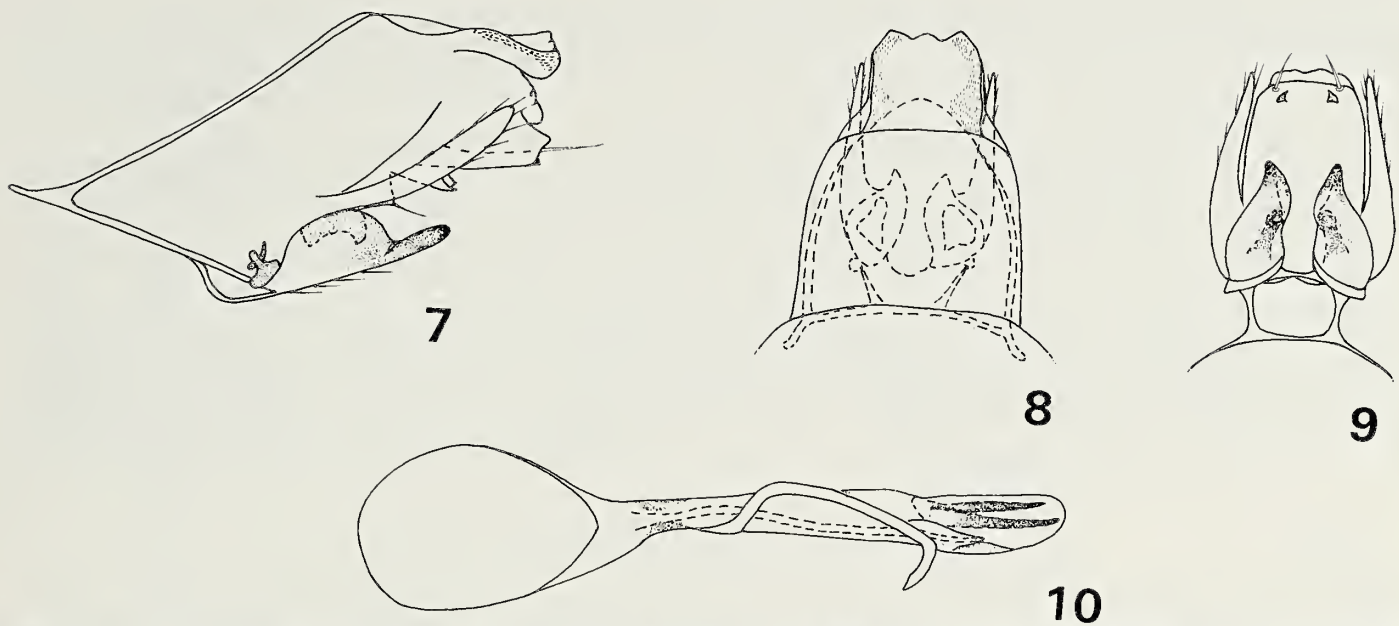


Fig. 7–10.—*Neotrichia nesiotes*, n. sp., male genitalia: 7, left lateral view; 8, dorsal view; 9, ventral view; 10, phallus, dorsal view.

Zumatrichia anomalopectera Flint

This species and *Z. antilliensis* Flint are among the most common Trichoptera on Grenada, and often fly together. Only males were identified and counted.

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Laboratory, 6 Jan. 1990, A. Thomas, (malaise trap), 1 male; same, 28 Jan. 1990, J. Telesford, 7 males; same, 29 Jan. 1990, A. Thomas, J. Telesford, 2 males; same, 31 Jan. 1990, M. Thomas, J. Telesford, 4 males; same, 1 Feb. 1990, A. Thomas, 3 males; same, 31 Jan. 1990, A. Thomas, 2 males; same, 19 Feb. 1990, R. E. Woodruff, 7 males; same, 22 Feb. 1990, R. E. Woodruff, 5 males; same, 23 Feb. 1990, R. E. Woodruff, 2 males; same, 6 March 1990, H. Thomas, 10 males; same, 13 March 1990, J. Telesford, 14 males; same, 6 May 1990, A. Thomas, (malaise trap), 5 males; same, 15 May 1990, A. Thomas, 25 males; same, 8 June 1990, J. Telesford, 87 males; same, 27 Sept. 1990, R. E. Woodruff, 2 males; same, 3 Oct. 1990, R. E. Woodruff, 2 males; same, 12 Oct. 1990, R. E. Woodruff, 2 males; Balthazar Estate, 1 June 1990, J. H. Frank, A. Thomas, 63 males; same, 12 June 1990, 44 males. PARISH ST. JOHNS: Grenville Vale, 3 Oct. 1990, R. E. Woodruff et al., 4 males; Black Bay, 26 Feb. 1990, R. E. Woodruff et al., 3 males (all in FSCA).

Neotrichia nesiotes, new species

Fig. 7–10

Diagnosis.—Distinguished by the shape of the subgenital plate of which the posterior tip is emarginate in lateral view and rounded in ventral view, by the narrow clasper with rounded apex, and by the phallus possessing two heavy, internal spines.

Description.—Male: Length of forewing, 2 mm. Color of wings in alcohol grayish brown, mottled. Male genitalia: Ninth segment with anterolateral projection short, slightly upturned. Tenth tergum membranous, quadrangular in lateral aspect, apex slightly incised. Subgenital plate broad, parallel-sided in ventral aspect, emarginate in lateral aspect; bearing a large spine at each posterolateral corner and a small triangular process anterior of spine. Bracteole transparent, long, narrow, slightly upturned with several setae on dorsal and ventral margins. Clasper half length of bracteole, apical half dark brown, narrow, tip rounded, basal half broad, with dark, heavily sclerotized, mushroom-shaped inner structure. Phallus with spiral process, and two dark, stout, inner spines almost completely covered by tubular membranous envelope.

Type specimens.—Holotype, male (FSCA): GRENADA, PARISH ST. ANDREWS: Balthazar Estate, 1 June 1990, J. H. Frank, A. Thomas. Paratypes: Same

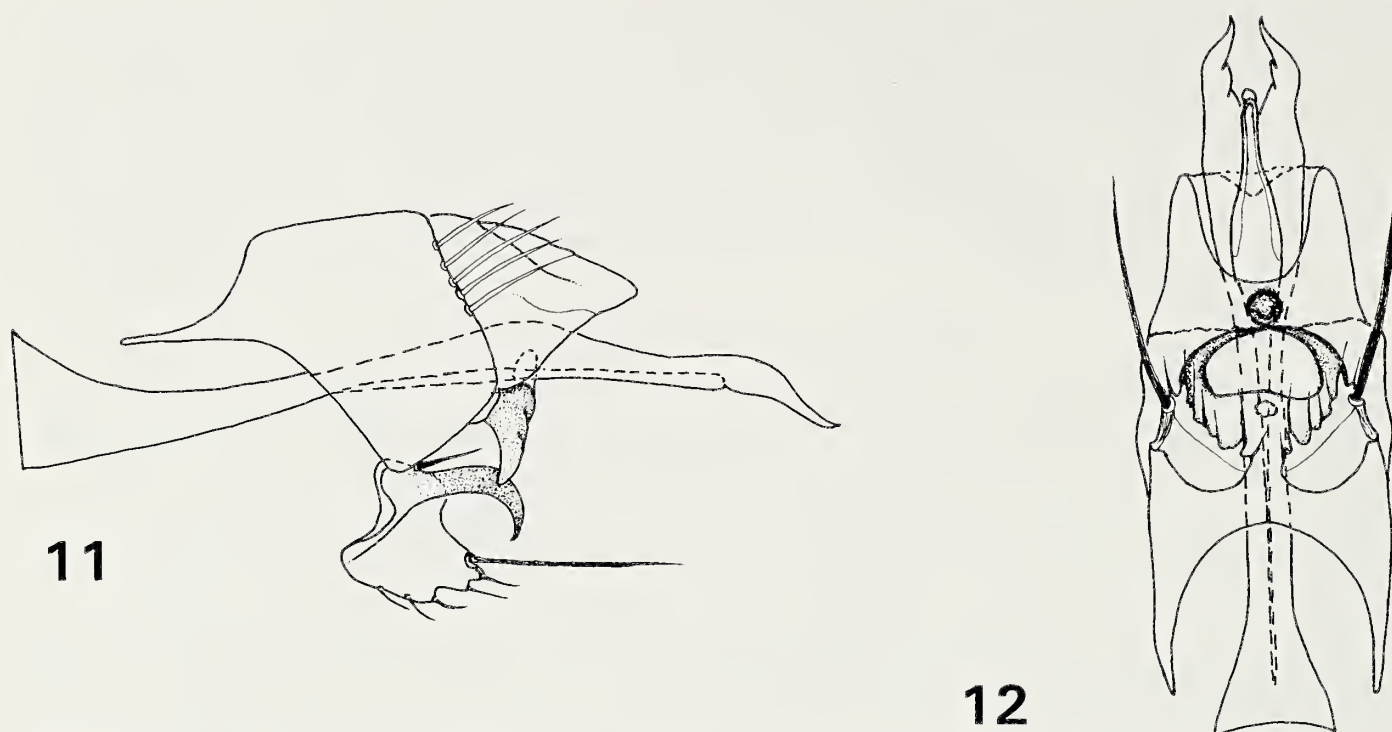


Fig. 11–12.—*Bredinia appendiculata*, n. sp., male genitalia: 11, left lateral view; 12, ventral view.

data, 3 males and 7 females (FSCA); same, 12 June 1990, 1 male and 1 female (NMNH); Mirabeau Agricultural Laboratory, 29 Jan. 1990, A. Thomas, J. Telesford, 1 female (FSCA); same, 1 Feb. 1990, A. Thomas, 1 male and 1 female (CMNH). PARISH ST. JOHNS: Black Bay, 26 Feb. 1990, R. E. Woodruff et al., 1 male (FSCA); Concord Falls, 20 Feb. 1990, R. E. Woodruff et al., 1 female (FSCA).

Etymology.—Greek: “islander,” referring to the habitat of this species.

Remarks.—This species is a member of the “*Exitrichia*” species group, related to *N. pequenita* Botosaneanu.

Neotrichia tauricornis Malicky

This species, which was described from the island of Guadeloupe, has been recorded from Martinique (Botosaneanu, 1989, 1990a) and recently from Colombia (Flint, 1991). Its presence on Grenada and St. Lucia is not surprising.

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Laboratory, 31 Jan. 1990, M. Thomas, 1 male and 1 female (FSCA); Windsor Estate, 6 March 1990, R. E. Woodruff et al., 1 male (FSCA). ST. LUCIA, QUARTER ANSE LA RAYE: 1 km SSW Anse La Raye (13°56'N, 61°03'W), 50 m, 21–30 June 1991, J. E. Rawlins, S. A. Thompson, 1 male (CMNH).

Bredinia appendiculata, new species

Fig. 11–12

Diagnosis.—From all known species *B. appendiculata* is easily distinguished by the very strong midventral hook of the subgenital plate, the long, pointed and mesally curved dorsal process of the clasper, and the broad, apical, caliper-like processes of the phallus.

Description.—Male: Length of forewing, 1 mm. Color in alcohol, fuscous, immaculate. Male genitalia: Ninth segment with anterolateral apodemes shorter than segment, broad basally. Tenth tergum in lateral aspect triangular and membranous, in dorsal aspect truncate apically. Subgenital plate hooklike, apex directed ventrad and bluntly pointed. Clasper trianguloid, ventral margin undulate,

setose, bearing apically a long, slender spine; dorsal portion sickle-shaped, pointed and curving ventromesally. Phallus tubular, apically divided into a bottle-shaped central tube flanked by broad, caliper-like processes surpassing central tube.

Type specimen.—Holotype, male (FSCA); GRENADA, PARISH ST. ANDREWS: Balthazar Estate, 1 June 1990, J. H. Frank, A. Thomas.

Etymology.—Latin: “with an appendix”, referring to a distinct, curved dorsal process of the clasper.

Remarks.—This, the second species described in the genus *Bredinia*, is similar to the type species (*B. dominicensis*) from Dominica. Studies underway with S. Harris show that the genus is also widespread and diverse (an additional eight species are known) on the continent.

Oxyethira azteca Mosely

This species has been recorded from Grenada from two localities: two miles west of Grand Etang and Balthazar (Flint, 1968). Two very similar species have been confused under the name *O. azteca* (Flint and Reyes, 1991). Both lots were restudied in light of this and both have been confirmed to be *O. azteca*.

Oxyethira janella Denning

This hydroptilid species is found from the southern United States, throughout Central America and northern South America, and on most of the islands of the Antillean Archipelago including Barbados (Botosaneanu, 1990a; Flint, 1968).

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Laboratory, 8 June 1990, J. Telesford, 1 male; Balthazar Estate, 12 June 1990, J. H. Frank, A. Thomas, 1 male; Windsor Estate, 6 March 1990, R. E. Woodruff et al., 2 males; Pearls Airport Area, 460 meters behind beach, 8 March 1990, R. E. Woodruff et al., 2 females. PARISH ST. JOHNS: Clozier, 27 Sept. 1990, R. E. Woodruff et al., 1 male (all in FSCA).

Orthotrichia tega Flint

Malicky (1983) recorded an unidentified species of *Orthotrichia* from Guadeloupe on the basis of nine females. He made available to the senior author several examples for study. They are identified as *Oxyethira tega* Flint. This species has minute ocelli, and occasionally even appears to lack them. This condition leads to misidentification. Malicky (1983) reported males of *Oxyethira tega* from his collection. The genus *Orthotrichia* should be deleted from the list of Lesser Antillean caddisflies, pending a new discovery.

Hydroptila grenadensis Flint

This species was described by Flint (1968) from Grenada, where it is frequently collected. It has recently been recorded from the continent in Panama, Colombia, Ecuador, Peru, and on Trinidad (Flint and Reyes, 1991).

Material.—GRENADA, PARISH ST. ANDREWS: Mirabeau Agricultural Laboratory, 28 Jan. 1990, J. Telesford, 1 male; same, 1 Feb. 1990, A. Thomas, 4 males; same, 6 March 1990, H. Thomas, 2 males; same, 13 March 1990, J. Telesford, 1 male and 1 female; same, 8 April 1990, J. Telesford, 2 males and 2 females; road end at Mt. St. Catherine, 22 Feb. 1990, R. E. Woodruff et al., 1 male; Windsor Estate, 6 March 1990, R. E. Woodruff et al., 1 male; Pearls Airport Area, 460 meters behind beach, 8 March 1990, R. E. Woodruff et al., 2 males and 3 females (all in FSCA); Grand Etang, 23–24 Oct. 1975, E. L. Todd, 1 male (NMNH).

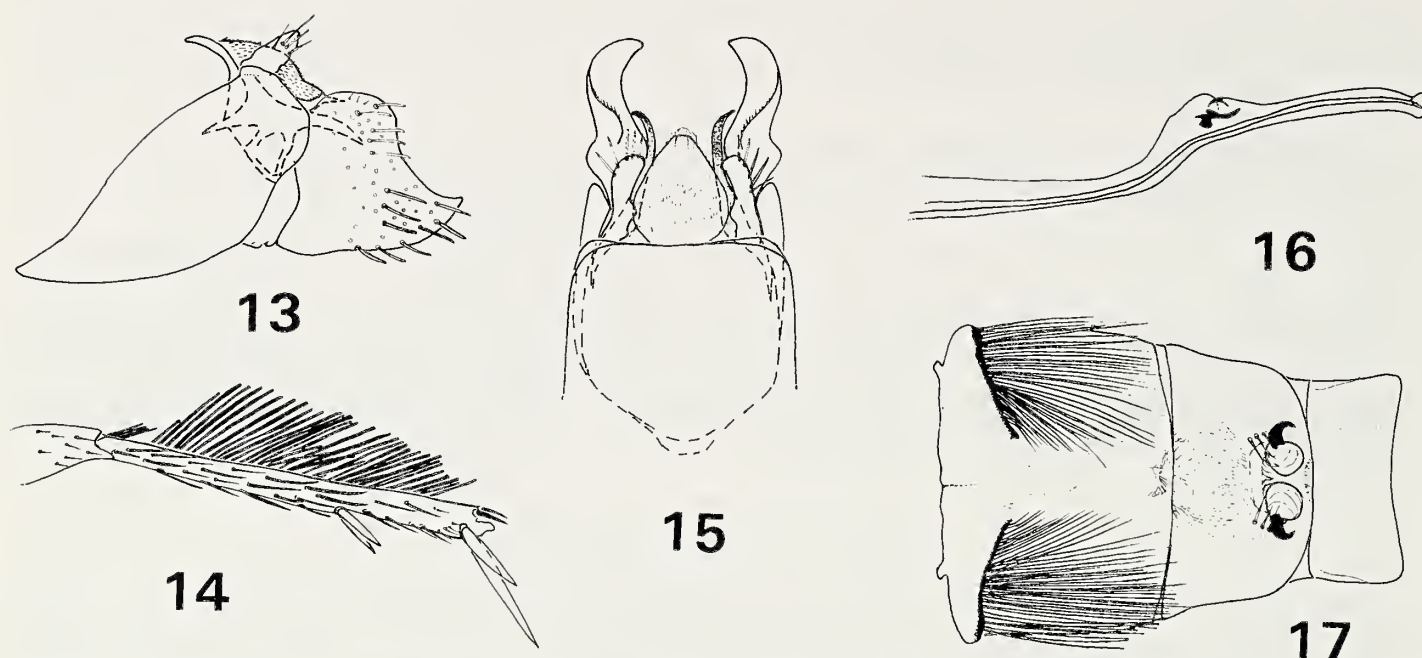


Fig. 13–17.—*Ochrotrichia (Metrichia) rawlinsi*, n. sp., 13, male genitalia, left lateral view; 14, midtibia, left lateral view; 15, male genitalia, dorsal view; 16, phallus, dorsal view; 17, posterior segments of abdomen, dorsal view.

Ochrotrichia (O.) ponta Flint

This species was described from Dominica, and recently recorded from Martinique and St. Vincent (Botosaneanu, 1990a). It is a new record for Grenada.

Material.—GRENADA, PARISH ST. ANDREWS: Road end at Mt. St. Catherine, 22 Feb. 1990, R. E. Woodruff et al., 1 male and 1 female (all in FSCA).

Ochrotrichia (O.), species

Dr. Malicky presented the senior author a female specimen of this genus and subgenus which was taken on Guadeloupe. Its genitalia are not similar to those of any other female *Ochrotrichia (O.)* described from the Lesser Antilles. It most likely represents an otherwise unknown species of the genus. It is recorded here to call attention to the occurrence of the typical subgenus on that island.

Material.—GUADELOUPE: Rivière Laurant, near Belleville, 8 Apr. 1979, Starmuhlner and Therzien, 1 female (NMNH).

Ochrotrichia (Metrichia) rawlinsi, new species

Fig. 13–17

Diagnosis.—This species differs from all known species of this subgenus mainly by bearing sclerotized “hooks” and membranous pouches on the sixth abdominal tergum and by the shape of the clasper with its distinct dorsal lobe and in the armature of the phallus.

Description.—Male: Length of forewing, 1.8 mm. Color of specimen in alcohol fuscous, with yellowish legs. Midtibia with a dense fringe of long, black, blunt hairs. Abdomen brownish with sixth and seventh terga constricted; a pair of dense, black hair tufts on the fifth tergum originating from the anterior section and covering most of the rest of the segment; sixth tergum small and trapezoidal with a pair of heavily sclerotized, black hooks attached to membranous pouches; seventh tergum small, butterfly-shaped. Male genitalia: Ninth segment in lateral aspect almost trapezoidal with anteroventral angle produced. Cercus short, semioval. Tenth tergum triangular in lateral aspect, covered with short spiculae; dorsolateral hook arising from a palmate, sclerotized base, produced into a long spine directed posteriad and curved slightly ventrad. Clasper broad, triangular with relatively prominent, rounded

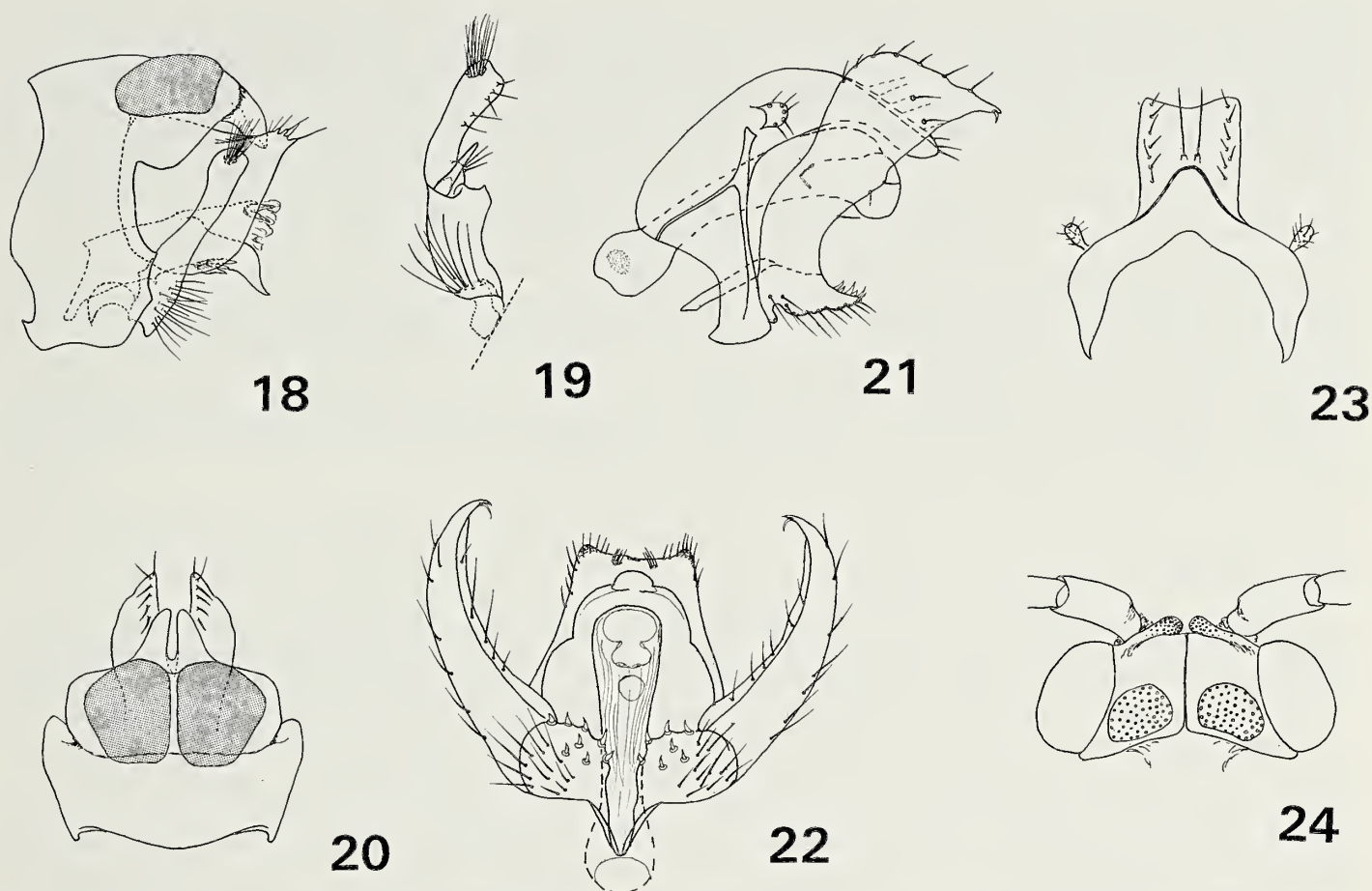


Fig. 18–24.—*Amphoropsyche woodruffi*, n. sp., male genitalia: 18, left lateral view; 19, clasper, posteroventral view; 20, ninth and tenth terga, dorsal view. 21–24.—*Helicopsyche grenadensis*, n. sp., male genitalia: 21, left lateral view; 22, posterior view; 23, ninth and tenth terga and cerci, dorsal view; head: 24, dorsal view.

dorsal lobe and pointed apicoventral lobe. Phallus with expanded base, bent sharply at $\frac{1}{4}$ distance from apex, with dark, sclerotized hook in bend, apex membranous with sclerotized central tubule.

Type specimen.—Holotype, male (CMNH); DOMINICA, PARISH ST. PAUL, Springfield Estate, 2.6 km ENE Canefield ($15^{\circ}21'N$, $61^{\circ}22'W$), 480 m, 13 June 1991, J. E. Rawlins, S. A. Thompson.

Etymology.—Named in honor of Dr. John E. Rawlins, Carnegie Museum of Natural History, who collected this species in Dominica.

Remarks.—This species is related to *O. (M.) exclamationis* Flint which is known only from Dominica.

Oecetis pratti Denning

This is the first record of the genus from Grenada. It was previously reported from Puerto Rico and Dominica (Flint, 1968).

Material.—GRENADA, PARISH ST. ANDREWS: Grand Etang, 23 Oct.–1 Nov. 1975, E. L. Todd, 6 females (NMNH).

Amphoropsyche woodruffi, new species

Fig. 18–20

Diagnosis.—Distinguished by the divided apico mesal process of the cerci and by short second segment of the clasper. The mesal lobe of the clasper is small, blunt and angled from caudal view.

Description.—Male: Length of forewing, 4.5 mm. Color in alcohol pale stramineous; hindwings with

both a strong, dark, basal hair-pencil and a fringe of long, dark hairs along posterior margin. Male genitalia: Ninth segment annular, anterior margin slightly sinuous. Cerci broad, fused mesally, apicomesally produced into a decumbent, lightly-sclerotized lobe, divided mesally from opposing lobe; internal amphora roughly elongate, oval. Tenth tergum divided to base mesally, lateral lobe very broad in lateral aspect, ventral margin rounded, apicodorsal margin with apex slightly produced and bearing a few spinous setae. Clasper with basal segment elongate, club-shaped in lateral aspect, with apical tuft of setae; in posteroventral aspect, inner margin of basal section broadly produced apicad with a small apical angle, second segment elongate, pointed, barely half length of apical section of first segment. Phallus with tubular phallobase; apex with a ventromesal process, pointed and angled ventrad in lateral aspect and bearing near base several spines on each side, dorsal portion membranous with a phallotremal sclerite, V-shaped in lateral aspect.

Type specimen.—Holotype, male (FSCA); GRENADA, PARISH ST. JOHNS: Concord Falls, 20 Feb. 1990, R. E. Woodruff et al.

Etymology.—Named in honor of Dr. R. E. Woodruff, Florida Department of Agriculture, who collected this new species on Grenada.

Remarks.—This species is most similar to *A. aragua* Holzenthal, although it is abundantly distinct in the various structures of the male genitalia. With *A. aragua* it shares the very broad, ventrally rounded tenth tergum which is not divided into two subequal processes. In *A. aragua* the cerci are fused and bear a single heavily-sclerotized apicomesal process, while in *A. woodruffi* the apicomesal process is divided mesally, very lightly sclerotized, and the tip is rounded. The second segment of the clasper is very long, almost attaining the apex of the first segment and the mesal lobe is produced into a strong, elongate point in *A. aragua*; in *A. woodruffi* the second segment is barely half the length apical portion of the first segment, and the mesal lobe is short and blunt.

Helicopsyche margaritensis Botosaneanu

This is a new record for Grenada. This species was previously known only from the Island of Margarita off the coast of Venezuela. Although characters of this example duplicate the illustrations of *H. margaritensis*, there are examples intermediate between it and *H. vergelana* Ross in many mainland populations in Panama, Colombia, Ecuador, Peru, and Venezuela. The resolution of species limits in this complex will require a careful revision of all the specimens and types that can be found.

Material.—GRENADA, PARISH ST. ANDREWS: Balthazar Estate, 12 June 1990, J. H. Frank, A. Thomas, 4 males and 1 female. PARISH ST. JOHNS: Grenville Vale, 3 Oct. 1990, R. E. Woodruff et al., 1 male and 1 female (all in FSCA).

Helicopsyche guadeloupensis Malicky

Helicopsyche, species 1: Flint, 1968:78 [new synonymy].

Helicopsyche, species 2: Flint, 1968:79 [probable synonym].

Originally described from Guadeloupe (Malicky, 1980), the species has since been recorded from Martinique (Botosaneanu, 1988, 1990a). Recent collections have uncovered it on St. Lucia. It is thus probable that the species recorded from St. Lucia (Flint, 1968), on the basis of a male without abdomen and some larvae, is this species. Certainly the larvae figured by Flint (1968:fig. 231) from St. Lucia and by Botosaneanu (1988:fig. 37) from Martinique are probably the same species. With the presence of *H. guadeloupensis* on both sides of Dominica confirmed, the single female recorded from that island as *Helicopsyche* species 1 (Flint, 1968) has been reexamined. The abdomen of that specimen is identical to the abdomens of females from St. Lucia and Martinique.

Material.—ST. LUCIA, QUARTER OF ANSE LA RAYE, Anse Galet, 1 km SSW Anse La Raye (13°56'N, 61°03'W), 21–30 June 1991, J. E. Rawlins, S. A. Thompson, 1 male and 1 female (CMNH). DOMINICA, Clarke Hall, 21–31 Jan. 1965, W. W. Wirth, light trap, 1 female (*Helicopsyche* sp. 1 of Flint, 1968) (NMNH). MARTINIQUE, Rivière Blanche au Pont d'Alma, 20 and 24 Feb. 1986, Botosaneanu, 1 male and 1 female (NMNH).

***Helicopsyche grenadensis*, new species**
Fig. 21–24

Diagnosis.—This species is a member of the *H. haitiensis* group, and is closely related to the Dominican species *H. apicauda* Flint. From the latter species it is most easily distinguished by the shape of the clasper, in which the dorsal margin is not so strongly rounded and the mesobasal lobe is shorter and pointed in lateral aspect.

Description.—Male: Length of forewing, 3 mm. Color in alcohol pale brown, unicolorous. Head with anteromesal setal warts borne on slender, cylindrical, mesally-directed processes. Third and fourth sterna reticulate, fifth sternum with a few basal reticulations; sixth sternum with a midventral process as long as sternum. Male genitalia: Ninth segment with anterior margin strongly produced laterally; lateral brace angled anteroventrally. Cercus small, oval, located slightly above lateral brace. Tenth tergum extending slightly beyond clasper in lateral aspect; in dorsal aspect parallel-sided, apex shallowly emarginate, with a row of setae along each side, with a basal V-shaped dark mark not extending down dorsum but bearing a pair of large, posteriorly-directed setae near midline. Clasper narrow, in lateral aspect dorsolateral lobe slightly bent near middle, narrowed above mesobasal lobe, anterodorsal angle rounded, posterodorsal angle produced into a point; mesobasal lobe fused to lateral lobe, pointed in lateral aspect, broad and rounded in posteroventral aspect, covered with short spines. Phallus only slightly curved, enlarged basally and apically; apex membranous with a darkened, internal phallotremal sclerite.

Type specimens.—Holotype, male (FSCA): GRENADA, PARISH ST. ANDREWS: Clabony, 12 Oct. 1990, R. E. Woodruff, A. Thomas. Paratypes (NMNH): Same data, 1 male and 1 female.

Etymology.—Latin: “from Grenada,” referring to the island where this species was collected.

Remarks.—The functional and taxonomic significance of the odd anteromesal setal wart of the head in this species is difficult to assess (Fig. 24). The heads of *H. vergelana* and *H. guadeloupensis* also possess this structure. Possibly it is present universally in the genus and is of no particular specific significance.

ACKNOWLEDGMENTS

The authors thank L. Botosaneanu, Instituut voor Taxonomische Zoologie, Universiteit Amsterdam, The Netherlands, and H. Malicky, Biologische Station Lunz, Lunz am See, Austria, for providing material for comparison or identification. We also acknowledge R. E. Woodruff, Florida Department of Agriculture, Gainesville, Florida, and J. E. Rawlins, Carnegie Museum, Pittsburgh, Pennsylvania, for making material under their care available to us.

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FIRST OCCURRENCE OF *SEYMOURIA*
(AMPHIBIA: BATRACHOSAURIA) IN THE
LOWER PERMIAN ROTLIEGEND OF
CENTRAL GERMANY

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ABSTRACT

The amphibian *Seymouria* is reported for the first time from outside of the Lower Permian of North America. Two specimens that include skulls and some postcrania are described from the Lower Permian Tambach Formation, lowermost unit of the Upper Rotliegend, of the Bromacker locality in the middle part of the Thuringian Forest near Gotha, central Germany. They are tentatively referred to *S. sanjuanensis*, known otherwise only from Lower Permian deposits of Wolfcampian age in southwestern United States. The *Seymouria* and several other tetrapods from the Bromacker locality form an assemblage that is found elsewhere only in the Lower Permian of the United States. The Bromacker tetrapod assemblage is, therefore, of great importance not only in assessing the biostratigraphic position and age of the Tambach Formation, but also in reconstructing distribution patterns of Early Permian vertebrates.

INTRODUCTION

Until very recently, all well-documented occurrences of the well-known amphibian *Seymouria* were restricted to the Lower and lowermost Upper Permian of the southwestern United States. The first described and most commonly encountered species, *S. baylorensis* Broili (1904), occurs mainly in the middle Leonardian age deposits of the lowermost horizon of the Clear Fork Group (Arroyo Formation) of north-central Texas. A detailed knowledge of the anatomy of *Seymouria* is based almost entirely on the description of this species by Watson (1918) and White (1939). On the basis of a dozen specimens, including skulls and partial postcrania, collected from the earlier deposits of the late Wolfcampian (earliest Permian) age Organ Rock Shale, Cutler Group of southeastern Utah, Vaughn (1966) described a second species, *S. sanjuanensis*. Six additional specimens of *S. sanjuanensis*, some essentially complete and all preserved in a single block from an early to middle Wolfcampian horizon in the Lower Permian Cutler Formation of north-central New Mexico, were described by Berman et al. (1987). Two other species of *Seymouria* have been described on the basis of poorly preserved and limited materials: *S. grandis* Olson (1979) from a late Leonardian age horizon of the Clear Fork Group (Vale Formation) of north-central Texas and *S. agilis* Olson (1980) from a lowermost horizon of the Upper Permian, Guadalupian age Flowerpot Formation of Oklahoma. A greater geographic distribution of *Seymouria* was noted by Langston (1963), who reported its occurrence in the Lower Permian red beds of Prince Edward Island of eastern Canada. Identification

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was based on a small, partial right femur he believed to be indistinguishable from that of *S. baylorensis*.

In a series of papers Martens (1988, 1989) and Boy and Martens (1991) reported a diverse assemblage of tetrapods (amphibians and reptiles) that are represented by articulated skeletal remains, as well as some invertebrates (conchostracans, insects, and myriapods) from a single site in the Lower Permian red-bed deposits of the Upper Rotliegend of Germany. The site, an abandoned sandstone quarry known as the Bromacker locality, is in the middle part of the Thuringian Forest, central Germany. The presence of vertebrate skeletal remains at the Bromacker locality was only recently discovered by Martens in 1974 (Martens, 1980). Two of the vertebrate specimens found at the Bromacker locality are described here as belonging to the amphibian genus *Seymouria*, and each includes a skull and some postcranial elements. The larger and better preserved of the two, which was earlier assigned to *Seymouria* by Martens (1988, 1989), is nearly indistinguishable from *S. sanjuanensis* from the Lower Permian of Utah and New Mexico (Vaughn, 1966; Berman et al., 1987).

The *Seymouria* reported here is part of a growing assemblage of terrestrial or semi-terrestrial tetrapods from the Bromacker locality that on the one hand is unique for western and central Europe, but on the other is quite typical of that found in widely separated Lower Permian deposits in the United States. The resemblance between the Bromacker and the United States tetrapod assemblages most likely reflects a similarity in environmental conditions, inasmuch as the sediments of the Bromacker locality, as well as the Upper Rotliegend in general, include typical fluvial red-bed facies like those in the Lower Permian of the United States (Martens, 1975, 1982, 1988, 1989; Martens et al., 1981). The Bromacker vertebrate assemblage, therefore, provides a unique opportunity to understand better the distributional patterns of Early Permian vertebrates across northern Pangaea.

The following abbreviations are used to refer to collection repositories: CM, The Carnegie Museum of Natural History, Pittsburgh; CNHM, Field Museum of Natural History, Chicago; MCZ, Museum of Comparative Zoology, Harvard; MNG, Museum of Nature, Gotha, Germany; NTM VP, Navajo Tribal Museum, Window Rock, Arizona; and TMM, Texas Memorial Museum, University of Texas, Austin.

Abbreviations used in figures are as follows: an, angular; art, articular; bps, basiparasphenoid complex; cl, clavicle; co, coronoid; d, dentary; f, frontal; il, ilium; it, space for intertemporal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pc, palpebral cup; pf, postfrontal; pm, premaxilla; po, postorbital; pra, prearticular; prf, prefrontal; psp, postsphenial; pt, pterygoid; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal; st, supratemporal; v, vomer.

GEOLOGY

The *Seymouria* specimens described here, as well as a variety of other tetrapods described or noted by Martens (1988, 1989) and Boy and Martens (1991), are from the Lower Permian Tambach Formation, Upper Rotliegend, of the Bromacker locality near the village of Tambach-Dietharz and about 20 km south of the town of Gotha in the middle part of the Thuringian Forest, central Germany (Fig. 1). The Bromacker locality has been long known as a very important locality for excellently preserved tetrapod trackways in the sandstones of the Tambach Formation since about 1885 (Pabst, 1896, 1908; Mueller, 1954, 1969; Haubold, 1971, 1973).

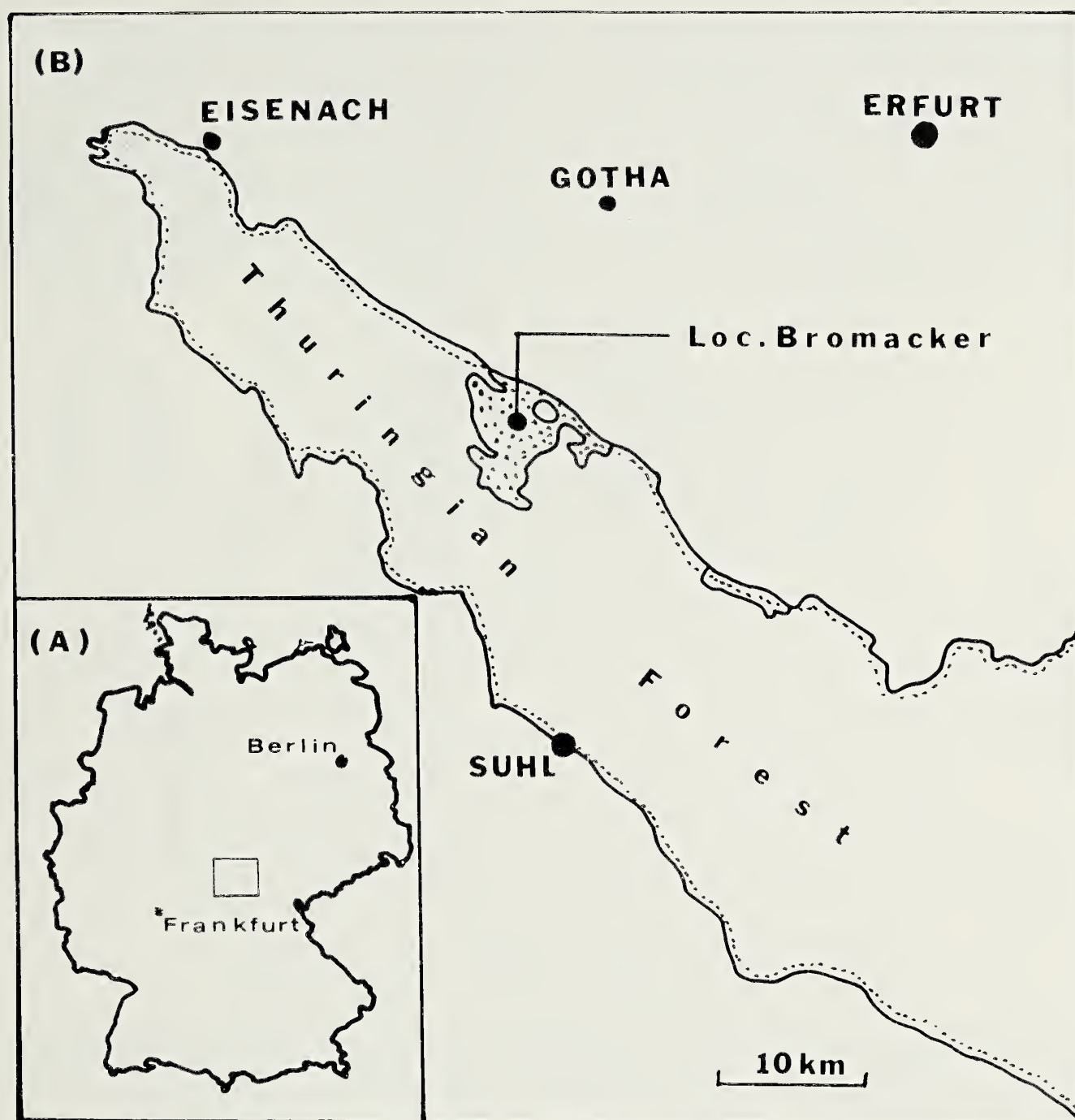


Fig. 1.—(A) Map of Germany with inset to show Thuringian Forest area. (B) Detailed map of the inset of (A) showing Bromacker locality and surrounding extent of Tambach Formation.

The stratigraphic section in the Thuringian Forest includes a succession of terrestrial formations of the Upper Carboniferous Stephanian and Lower Permian (Lower and Upper Rotliegend) that lies disconformably on crystalline basement rocks of the Hercynian orogen and are overlain in places by the Upper Permian marine Zechstein. The Stephanian-Rotliegend sediments of the Thuringian Forest were deposited in an intramontane basin sometimes referred to as the Thuringian Forest Basin. This basin, however, is actually the southwestern portion of a larger, northeast-trending basin, the Saale Basin, which extends about 200 km to the northeast to also include the Halle Basin. Upper Carboniferous and Lower Permian deposits of the Saale Basin, as well as other intramontane basins of central and western Europe, originated from the erosion of the rising Hercynian orogen and the filling associated with subsiding depressions and fault blocks. It is important to note that the Rotliegend, as well as its subdivision into lower and upper units, is a traditional lithostratigraphical unit that refers to continental beds of uppermost Carboniferous and Permian age in central Europe. In western Europe

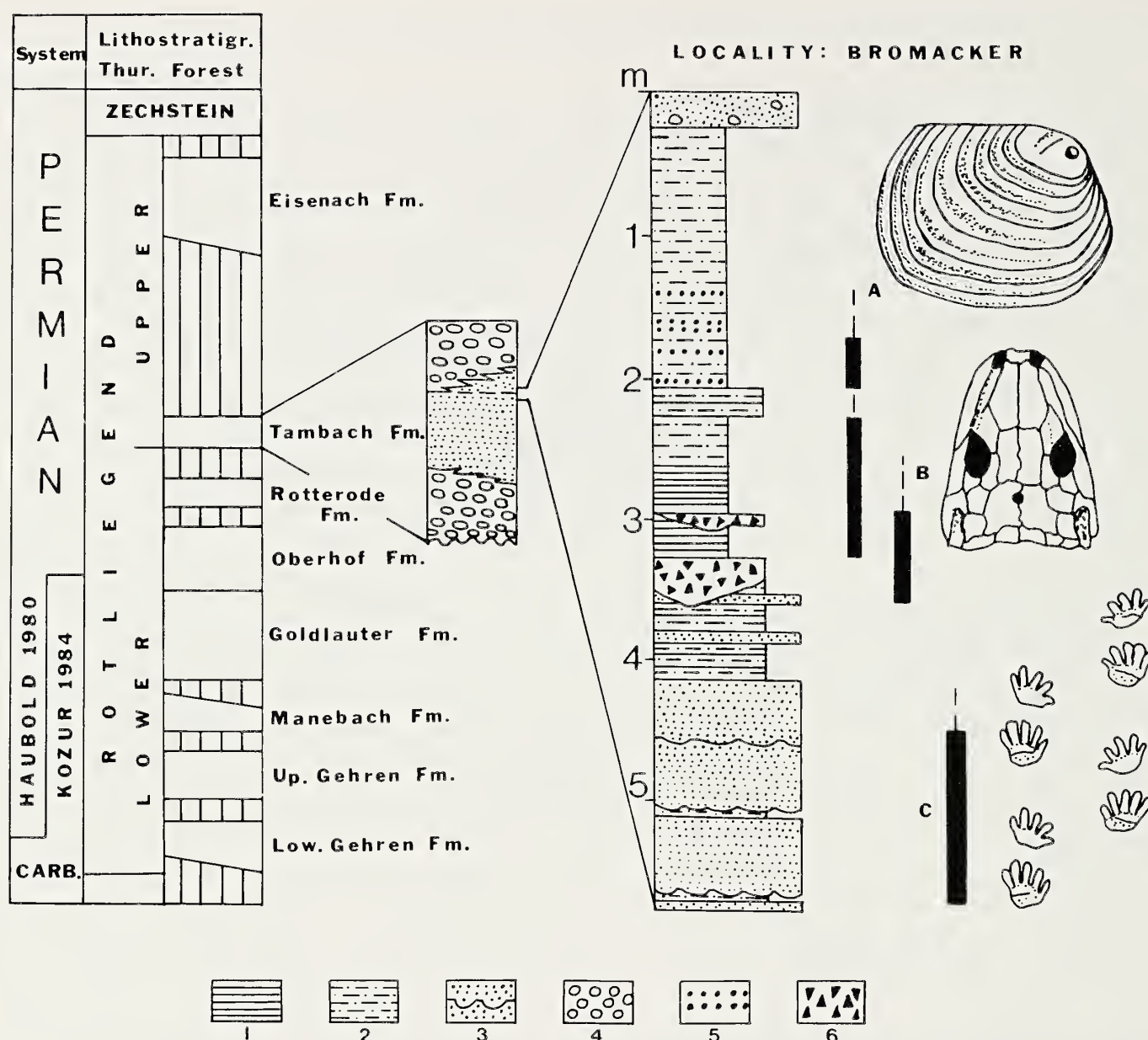


Fig. 2.—Generalized lithostratigraphic model of the Permo-Carboniferous of the Thuringian Forest area of central Germany. Levels of the Permo-Carboniferous boundary proposed by Haubold (1980) and Kozur (1984) are indicated. Lithofacies of the Tambach Formation in general and of the exposed section at the Bromacker locality in detail are shown; indicated lithofacies include: 1, laminated siltstone; 2, siltstone; 3, fine-grained sandstone with mudcracks; 4, conglomerate; 5, calcareous concretions; 6, clay-pebble conglomerate. Vertical bars A, B, and C indicate levels of occurrences of conchostracans, tetrapod skeletons, and tetrapod trackways, respectively.

the lithostratigraphic terms Autunian (derived from the Permian basin near Autun, France) and Saxonian (derived from the Sachsen-Anhalt region in central Germany) are used commonly to replace Lower and Upper Rotliegend, respectively.

Exposures at the Bromacker locality (Fig. 2) are limited to the Tambach Formation, which is the lowermost formational unit of the Upper Rotliegend in the Thuringian Forest. The Tambach Formation consists of typical red-bed fluvial deposits that can be divided into three major units: a basal conglomerate unit, an approximately 60 m thick middle sandstone unit, and an overlying typical fanglomerate unit. Only the uppermost level of the middle sandstone unit is exposed in the Bromacker quarry. Within this level a general sequence of three distinct fluvial facies can be recognized, each containing particular types of fossils. The lower third of the section consists of thick-bedded sandstones. They contain

thin intercalations of silty mudstones that originated from (?seasonal) floods and possess mudcracks and tetrapod trackways. In the middle portion of the section are flat-bedded channel fills consisting mainly of mudstones containing clay-pebble conglomerates. These channels contain the tetrapod skeletal remains discussed in this report. The upper half of the section consists of shaly siltstones, in part laminated and rich in mica, with layers of lenses of fine-grained sandstones. They were deposited on a fluvial floodplain with ephemeral bodies of quiet water and contain layers rich in conchostracans and some remnants of insects.

SYSTEMATIC PALEONTOLOGY

Order Batrachosauria

Suborder Seymouriamorpha

Family Seymouriidae

Genus *Seymouria* Broili, 1904

Seymouria cf. *S. sanjuanensis* Vaughn, 1966

Specimens.—This study is based on two specimens of *Seymouria*. One, MNG 7727, consists of the greater part of a skull, measuring about 56 mm in length, with both jaws closely attached, and isolated but closely associated right clavicle and ilium (Figs. 3–8). MNG 7727 was discovered in 1986 and identified as *Seymouria* in subsequent reports by Martens (1988, 1989). The second and much smaller specimen, MNG 8759, is reported here for the first time. It is a partial, articulated skeleton consisting of a complete skull, measuring about 21 mm in length, with closely applied jaws, shoulder girdle, and partial forelimbs.

Horizon and locality.—Uppermost level of 60 m thick middle sandstone unit of the Lower Permian Tambach Formation, Upper Rotliegend, in the Bromacker locality of the middle part of the Thuringian Forest near the village of Tambach-Dietharz and about 20 km south of the town of Gotha, central Germany. The German specimens are compared with those of *S. sanjuanensis* and *S. baylorensis* from the Lower Permian of the southwestern United States and some confusion may arise regarding the stratigraphic levels of those specimens from Texas, because the previously and long-used scheme of formational names (Plummer and Moore, 1921; Romer, 1974) has been recently revised by Hentz (1988). Throughout the text, therefore, where there is a conflict between the two nomenclatures, the newer scheme is followed parenthetically by the older one.

DESCRIPTION AND COMPARISON

Unless otherwise stated the following description of the German *Seymouria* will be based on specimen MNG 7727, which consists of most of the skull with lower jaws, right clavicle and ilium (Fig. 3–8). The skull has undergone considerable dorsoventral flattening and undistorted would have probably had a rather box-like structure at least in the postorbital region, with the cheek and skull table joining at almost a right angle. Although most of the dermal roofing bones are represented, only the left side of the skull is nearly intact. Here the intertemporal was displaced a few millimeters dorsal to the skull roof and removed subsequently during preparation, and the tabular and postparietal are lost. The presence, shape, and relationships to adjoining bones of the left intertemporal are easily established, however, because the bones surrounding it have retained almost exactly their original positions. Of the right side of the skull roof, the premaxilla, nasal, greater part of the lacrimal, and anterior portion of the dentary are in place, the postfrontal,



Fig. 3.—*Seymouria* cf. *S. sanjuanensis* MNG 7727. Photograph showing skull in dorsal view.

jugal, and postorbital have been displaced a short distance and are exposed in internal view, and the frontal, parietal, postparietal, postfrontal, temporal series, squamosal, and quadratojugal are missing or simply cannot be identified among the jumble of bones just posterior to the skull.

All the sutures are open and very easily traced. The sculpturing is moderately developed and present in all areas where it would be expected. There are no indications of a lateral line structure except possibly for a pronounced, smooth groove along the orbital margin of the postorbital. It ends abruptly, however, at the margins of the bone. A similar channel is only vaguely recognizable in specimens of *S. sanjuanensis*. The approximately 56 mm overall length of the skull is quite small, only about 64% of that of the smallest known North American specimens (Berman et al., 1987). The small size, moderately developed sculptur-

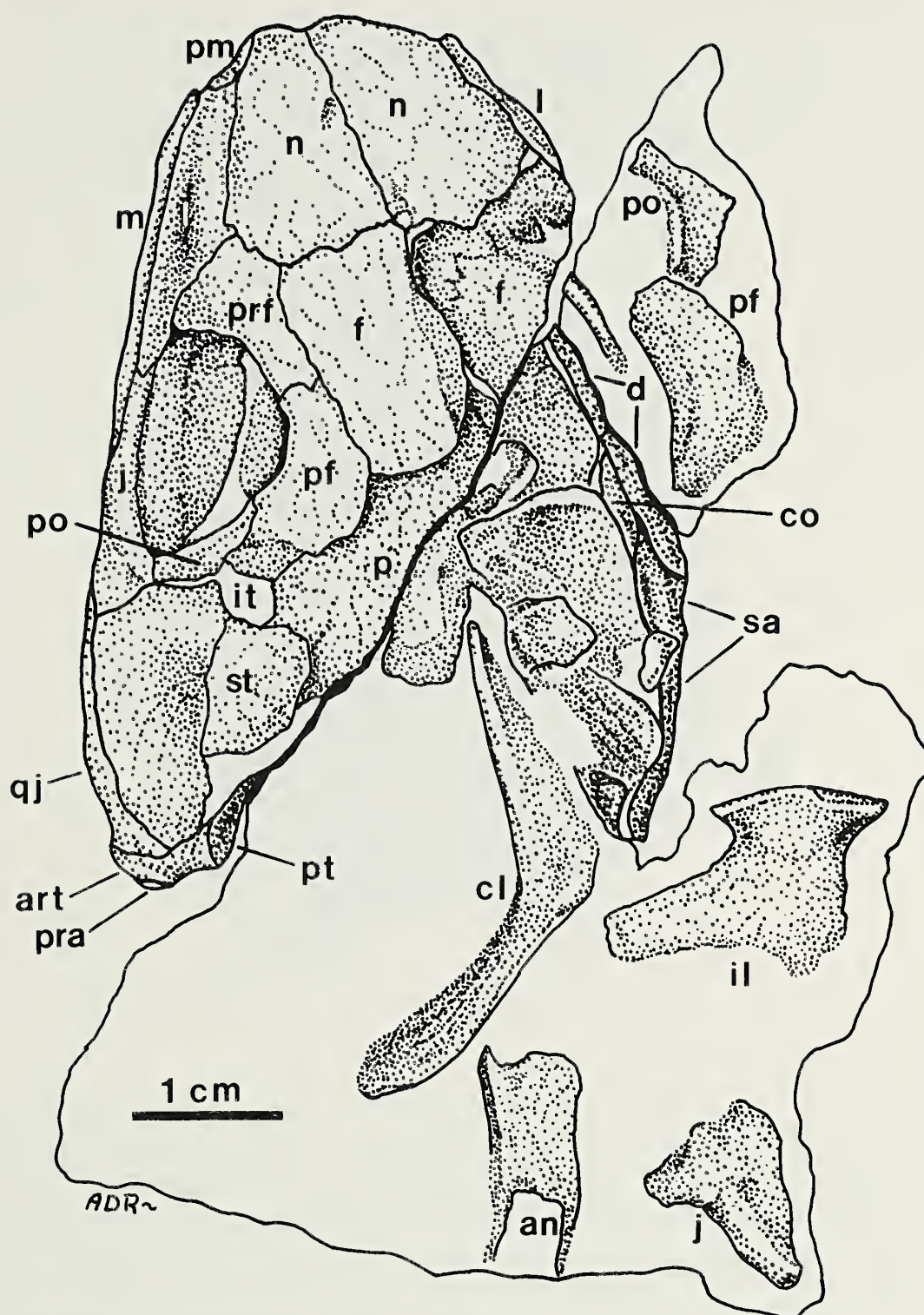


Fig. 4.—*Seymouria* cf. *S. sanjuanensis* MNG 7727, as seen in Fig. 3.

ing, open sutures, and postmortem movement of many skull roof elements suggest that MNG 7727 was probably not fully matured. The other *Seymouria* specimen from Germany, MNG 8759, is much smaller, with an overall skull length of only 21 mm. The dermal bones of the skull and shoulder girdle are very poorly ossified, lack sculpturing, appear often as a thin veneer or impression, and are commonly loosely or narrowly disarticulated; the limb elements are also very poorly ossified and exhibit no detailed structure. These features strongly suggest that MNG 8759 represents a very immature stage of development, probably postlarval.

Enough of the skull of MNG 7727 is preserved to see that it very nearly duplicates the anatomy of *S. sanjuanensis* and to a lesser degree that of *S. baylorensis*. The two other described species of *Seymouria*, *S. grandis* (Olson, 1979) and *S. agilis* (Olson, 1980), though poorly known, exhibit features that readily



Fig. 5.—*Seymouria* cf. *S. sanjuanensis* MNG 7727. Photograph showing skull in ventral view.

distinguish them as distantly related and are, therefore, not considered here. In view of the availability of detailed descriptions with reconstructions of *S. sanjuanensis* (Vaughn, 1966; Berman et al., 1987) and *S. baylorensis* (White, 1939), the description given here will be limited primarily to a comparison of those features that provide a basis for taxonomic assignment of the German specimens.

Berman et al. (1987) recognized two derived cranial characters to distinguish *Seymouria sanjuanensis* from *S. baylorensis*, using primitive temnospondyls and batrachosaurs as outgroups for determination of character polarities. In *S. sanjuanensis* the postorbital differs in being a very narrow, chevron-shaped element, with the limbs of the chevron extending farther along the dorsal and ventral margins of the orbit and the posterior projecting apex partially separating the intertemporal and squamosal. In contrast, the postorbital in *S. baylorensis* is subrectangular with only a slightly convex posterior margin that barely projects between the intertemporal and squamosal, and contributes far less dorsally and ventrally to the orbital rim. The postorbital of MNG 7727 appears to be identical to that of *S. sanjuanensis* and, as in this species, the distal end of the dorsal limb of the left postorbital just reaches the dorsal margin of the orbit by encroaching along the orbital border of the prefrontal. The full extent of the ventral limb of the left postorbital, however, is not visible, as dorsoventral crushing of the skull has displaced it along the medial surface of the jugal. The isolated right postorbital, however, clearly shows that the dorsal and ventral limbs are subequal in devel-

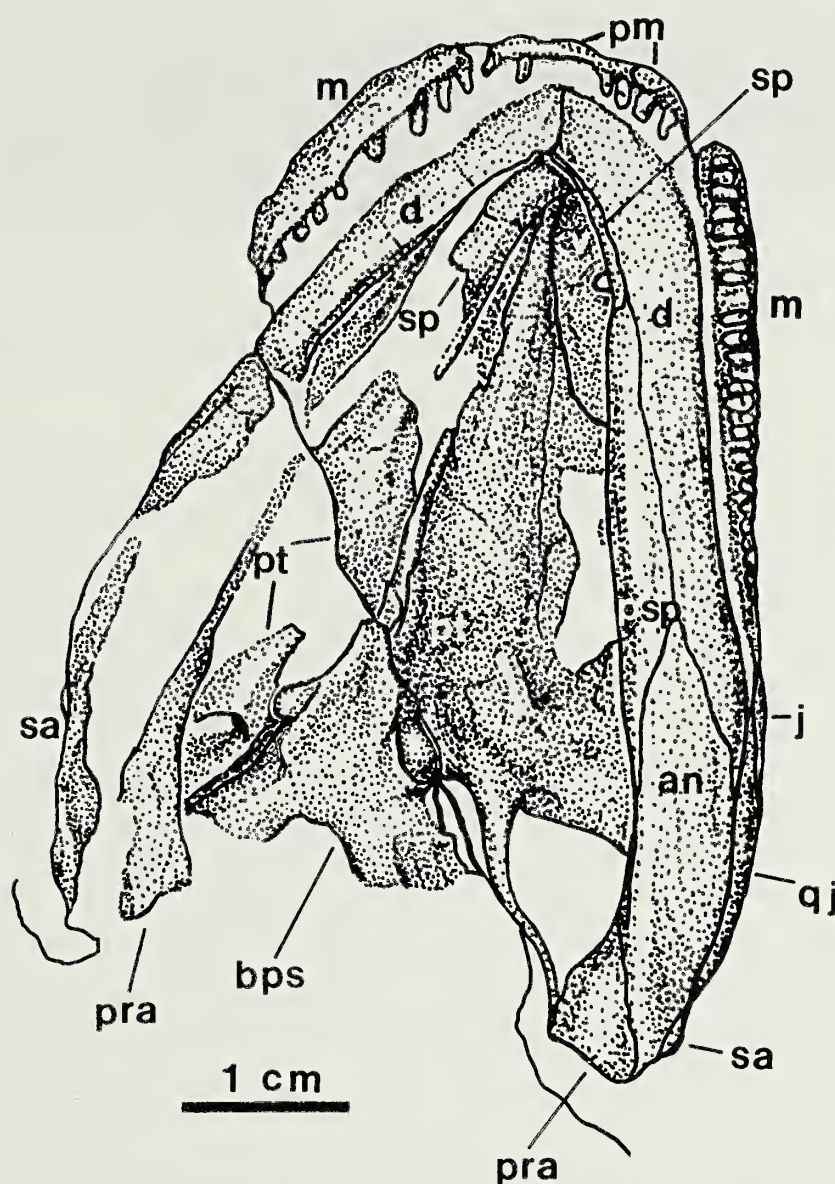


Fig. 6.—*Seymouria* cf. *S. sanjuanensis* MNG 7727, as seen in Fig. 5.

opment. A second derived feature of *S. sanjuanensis*, the separation of the maxilla and quadratojugal by the jugal along the ventral margin of the dorsal skull roof, also occurs in MNG 7727. The loss of contact between these two bones in *S. baylorensis* is apparently accomplished by a reduction in the anterior extent of the quadratojugal, rather than the posterior extent of the maxilla. In *S. baylorensis* the quadratojugal reaches to about the level of the midlength of the orbit, whereas in *S. sanjuanensis* and MNG 7727 it extends anteriorly to only just beyond the posterior border of the orbit.

Several primitive features that separate *Seymouria sanjuanensis* from *S. baylorensis* were interpreted by Berman et al. (1987) as stages in morphological trends in *Seymouria*. Two of these are difficult to interpret in MNG 7727 because of the incompleteness of the skull. A diagnostic feature originally used by Vaughn (1966) to distinguish the Utah specimens he assigned to *S. sanjuanensis* from *S. baylorensis* and later also utilized by Berman et al. (1987) in assigning New Mexico specimens to the same species was the greater anteroposterior extent of the postparietals. This feature was measured as the percent of the total length of the skull occupied by the postparietals. In *S. sanjuanensis* the postparietals are 10.2–11.1% of the skull length, whereas in *S. baylorensis* they are 8.9–9.6% (Berman et al., 1987). Though the postparietals are absent in MNG 7727, a restoration of this



Fig. 7.—*Seymouria* cf. *S. sanjuanensis* MNG 7727. Photograph showing skull in lateral view.

area of the skull table that assumes no radical differences from those of either species yields a value (Table 1) slightly greater and, therefore, closer to that for *S. sanjuanensis* than for *S. baylorensis*.

Differences in the structure of the supratemporal and tabular also distinguish the two species. In *S. baylorensis* the posterolateral corner of the supratemporal and the adjacent lateral margin of the tabular are greatly expanded as a well-developed process that is bent sharply ventrally and sculptured externally. Anterior to and continuous with the downturned process of the lateral margin of the supratemporal is a narrow, vertical otic shelf that projects from the lateral margin of the ventral surface of the supratemporal. Its smooth external surface is continuous with that of the squamosal bordering the otic notch. On the other hand, in *S. sanjuanensis* the same process of the supratemporal and tabular is only slightly developed and extends only slightly ventrolaterally. The smooth, vertical otic shelf of the supratemporal extends to the posterolateral corner of the bone. Although the tabular is missing in MNG 7727, the supratemporal is complete and exhibits only the slightest indication of a laterally downturned process of its posterolateral corner. The smooth, vertical otic shelf of the supratemporal tapers posteriorly to a point as it nearly reaches the end of the slightly downturned, posterolateral corner of the bone.

Four closely related differences of the maxilla and its dentition not only distinguish between *Seymouria sanjuanensis* and *S. baylorensis*, but also demonstrate that the former is more primitive (Berman et al., 1987). These differences were interpreted as representing morphological trends in the genus and include: 1) reduction in the number of teeth, 2) overall increased size of the teeth, 3) increased heterodonty of the "canine" region, and 4) increased height of the maxilla. Berman et al. (1987) presented a series of four groups of *Seymouria* specimens to illustrate these trends that included, arranged in order of increasing degree of advancement

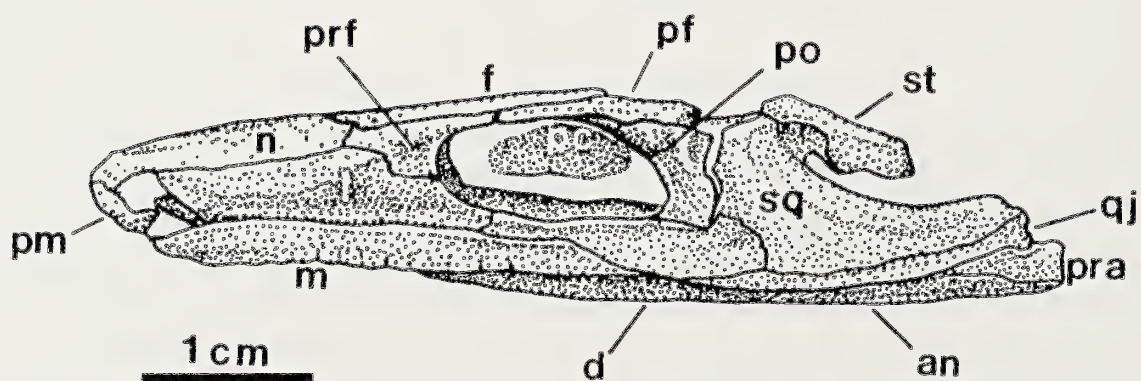


Fig. 8.—*Seymouria* cf. *S. sanjuanensis* MNG 7727, as seen in Fig. 7.

Table 1.—Comparative skull dimensions (in mm) of specimens of *Seymouria*. Those for *S. sanjuanensis* from New Mexico (CM 38022, 28596, 28597) and Utah (NTM VP 1023, 1024, 1025, 1034) and *S. baylorensis* from Texas (CNHM 663; MCZ 1081, 1082, 1083, 1085) except TMM 31189-1 are given as averages based on data from Berman et al. (1987). All proportions are given as percentages. Abbreviations: e, estimated; MxD, maxillary depth; MxL, maxillary length; MxT, number of maxillary teeth; PpL, postparietal length; SkL, skull length.

Specimens	SkL	PpL	$\frac{PpL}{SkL}$	MxD	MxL	$\frac{MxD}{SkL}$	MxT	$\frac{MxL}{MxT}$ SkL
<i>Seymouria sanjuanensis</i>								
New Mexico	89	9.3	10.5	7.7	51	8.5	29	2.0
Utah	89	10.0	11.1	10.0	51	11.0	25	2.3
<i>Seymouria baylorensis</i>								
Texas, TMM 31189-1	99	9.3	9.4	9.8	58	10.0	21	2.8
Other Texas specimens	111	10.5	9.3	15.0	60	13.5	17	3.2
<i>Seymouria</i> cf. <i>S. sanjuanensis</i>								
MNG 7727	56	e7.0	12.5	3.7	30	6.6	24	2.2

and general stratigraphic sequence from the lowest occurrence: 1) *S. sanjuanensis* specimens from the early to middle Wolfcampian (earliest Permian) age Cutler Formation of New Mexico (Berman et al., 1987); 2) *S. sanjuanensis* from the late Wolfcampian age Organ Rock Shale, Cutler Group of Utah (Vaughn, 1966, 1970; Blakey, 1980); 3) *S. baylorensis* skull TMM 31189-1 from the latest Wolfcampian age Nocona Formation (Admiral Formation), Wichita Group of Texas. Though this specimen is intermediate between *S. sanjuanensis* and *S. baylorensis* in several characters, Berman et al. (1987) referred it to the latter species on the basis of its closer overall form; it is, therefore, the only Texas specimen of *S. baylorensis* represented by good cranial material not from the Clear Fork Group; and 4) *S. baylorensis* specimens from the middle Leonardian age, lowermost level of the Clear Fork Group (Arroyo Formation) of Texas (Williston, 1911; White, 1939). Measurements expressing the trends of the dentary and its dentition are given in Table 1 as averages for each of the four groups of *Seymouria* specimens listed above (based on data from Berman et al., 1987) and the German specimen MNG 7727.

Of the upper marginal dentitions, only those of the premaxillae and left maxilla are complete in MNG 7727. As in *Seymouria sanjuanensis* and *S. baylorensis*, the premaxilla of MNG 7727 possesses, or has spaces for, six subequal teeth, but as expected they are considerably smaller, having a maximum length of about 1.8 mm and a maximum basal diameter of about 1.0 mm. The complete left maxilla of MNG 7727 possesses 25 teeth, or tooth positions, which equals the average value for specimens of *S. sanjuanensis* from the late Wolfcampian of Utah, but is well above those values for specimens of *S. baylorensis*.

Following Vaughn (1966), Berman et al. (1987) employed two sorts of calculations to demonstrate differences in the relative developments of the maxillary dentitions of specimens of *S. sanjuanensis* and *S. baylorensis*. One calculation used was the percent ratio of the average unit length of the maxilla per tooth to overall skull length. As indicated in Table 1, there is a marked separation between the average values for specimens of *S. sanjuanensis* and *S. baylorensis*; MNG 7727 lies within those of the former. Differences in the relative sizes of individual teeth of the maxillary dentitions of *S. sanjuanensis* specimens CM 28596 from

New Mexico and NTM VP 1034 from Utah, and *S. baylorensis* specimens TMM 31189-1 and MCZ 1028 from Texas were also depicted graphically by plotting the ratio of their basal diameters (rather than tooth length since crowns are seldom preserved) to skull length. The advantage of this measurement is that it allows a direct comparison of the relative development of not only the dentitions in general, but of specific regions. The values obtained for the largest "canine" tooth of the maxillary series of each of the above specimens were 0.020, 0.017, 0.033, and 0.040, respectively, indicating a noticeable increase in the relative sizes of the teeth in the "canine" region. The same measurements for the eleventh tooth of the same series of maxillae are 0.010, 0.012, 0.022, and 0.026, respectively, indicating not only that the cheek teeth of *S. sanjuanensis* are relatively smaller than those of *S. baylorensis*, but also that in this series of specimens the rate of increase in the relative sizes of the cheek teeth is less than that of the "canine" teeth. Applying the same method of calculating relative tooth size to the German *Seymouria* MNG 7727, the largest tooth of the "canine" region, the fifth, has a value of 0.018 and the eleventh tooth 0.011. These values are essentially the same as those for the *S. sanjuanensis* specimens CM 28596 and NTM VP 1034.

As would be expected, with the increased development of the maxillary dentitions in the *Seymouria* species of North America there is a general increase in the depth of the maxilla to accommodate them, particularly at the level of the "canine" region. In Table 1 this is expressed as the percent ratio of the maximum depth of the maxilla to the total skull length. Although the separation of values for the two species of *Seymouria* is not decisive due primarily to the intermediate value for *S. baylorensis* specimen TMM 31189-1, *S. sanjuanensis* is clearly the more primitive species in this feature. The value for MNG 7727 is slightly lower and, therefore, may represent a more primitive state of development.

There is one other difference between specimens of *Seymouria sanjuanensis* and *S. baylorensis* that has not been described in earlier comparisons. Casual inspection of the sutural patterns of the skulls of both species indicates a consistent difference in the relative positions of the anteriormost extents of the squamosals, intertemporals, and parietals. In *S. sanjuanensis* these bones reach, nearly reach, or extend just beyond the level of the posterior border of the orbit, whereas in *S. baylorensis* they end well behind the orbits. These two sutural patterns appear to reflect a difference in the relative elongation of the skull that is confined to a narrow, transverse band immediately posterior to the orbits. The difference in the relative elongation of the skull in this region can be demonstrated by expressing the distance between the otic notch and the orbit as a percent ratio to skull length. Though the differences between the average values of about 14.4 (range approximately 12.5–16.7) for the New Mexico and Utah specimens of *S. sanjuanensis* and 18.5 (range approximately 17.4–19.1) for the Texas specimens of *S. baylorensis* is small, they do not appear to overlap. On the basis of the general condition in primitive temnospondyls and batrachosaurs, the shorter postorbital region with a more forward position of the squamosals, intertemporals, and parietals in *S. sanjuanensis* is considered primitive. Although there has been some displacement of the skull elements in the postorbital region of the German specimen MNG 7727, it appears to duplicate *S. sanjuanensis* in this feature, with an estimated value for the above calculation of 12.3.

Near the upper margin of the left orbit in MNG 7727 is a large, semicircular plate of bone that appears to represent part of a palpebral cup. This structure has not been previously described in *Seymouria*.

The palate of MNG 7727 is partly obscured by the closely attached jaws, and that which is visible is badly fractured, with portions missing or slightly displaced. A greater portion of the left side of the palate is exposed, but only the suture separating the pterygoid and vomer is detectable. Only the crown of the vomerine tusk is visible, protruding medially above the splenial of the lower jaw (Fig. 5, 6). As in all species of *Seymouria*, the palate is completely closed by the pterygoids and vomers, which are covered by a shagreen of teeth. The pterygoid portion of the basipterygoid articulation is formed by a well-developed, semi-hemispherical, cup-like structure that projects ventrally and is open medially and dorsally. Also as in other *Seymouria* species, the pterygoid is unusual in forming a straight, transverse anterior border of the subtemporal fossa. With the exception of the shagreen teeth, these features of the palate are preserved in the smaller German skull MNG 8759.

The only identifiable portion of the braincase of MNG 7727 is an essentially complete basiparasphenoid complex; the jumble of mainly unidentifiable elements at the posterior margin of the skull may include other portions of the braincase. The basiparasphenoid conforms very closely to that in *Seymouria* except for one seemingly obvious difference, the structure of the cultriform process of the parasphenoid. White (1939) described the cultriform process in *S. baylorensis* as being a very short, broad, triangular process in ventral view, extending only about 15 mm beyond the basipterygoid processes and contacting along its lateral margins the pterygoids to help close the interpterygoid vacuity. This appears to be the same structure of the parasphenoid seen in *S. sanjuanensis*. The cultriform process of MNG 7727 is identical to that of both *Seymouria* species except for a narrow, additional distal portion that approximately doubles the relative length of the process. The anterior portion of the process has the typical V-shaped cross-section, with the apex directed ventrally. Though the palate is poorly preserved, it can be seen that at least in some places the pterygoids partially overlapped the ventrolateral margins of the process. Therefore, it is not certain whether the anterior portion of the cultriform process in MNG 7727 would be visible in an undisturbed specimen. The presence of a long cultriform process in MNG 7727, if actually absent in other *Seymouria* species, would set it apart as more primitive. Posterior to the basipterygoid processes the parasphenoid in *Seymouria* forms greatly expanded, lateral wings that cover the anterior half of the ventral surface of the otic capsule (White, 1939). Only the right lateral portion of the parasphenoid is complete in MNG 7727, and, though it exhibits a similar extensive outward expansion, its full extent anterolaterally is obscured by the quadrate ramus of the pterygoid. The midline portion of the parasphenoid between the posterolaterally diverging cristae ventrolaterales is apparently incomplete.

The lower jaws are in place and closely appressed to the outer margins of the palate and have rotated slightly on their long axis so that the lateral surface faces ventrally. The left jaw is complete, whereas in the right the region of the splenial and postsplenial is incomplete and slightly displaced and the incomplete angular lies a short distance behind the skull. It is not possible to expose the dorsomedial margin, including the adductor fossa, of either jaw; the dorsolateral margin and its dentition of each jaw is also hidden from view except for the posterior end of the right jaw. This exposure results from the absence of the cheek area of the skull roof. Features of the exposed areas of the jaws are well preserved and exhibit no noticeable deviations from the description given by White (1939).

The isolated right clavicle and ilium are located directly behind the skull. The

clavicle is complete and exposed in dorsal and medial views; it exhibits no noteworthy differences from that of *Seymouria* except for possibly the ventral spatulate blade being relatively slightly narrower in anteroposterior breadth. The nearly complete ilium is exposed in medial view and only the thin dorsal margin of the dorsal blade is incomplete. As in *Seymouria*, there is a well-developed posterior process, but that in MNG 7727 differs slightly in having a narrowly rectangular rather than triangular outline and in being directed posterodorsally rather than posteriorly.

SYSTEMATIC PLACEMENT

The German *Seymouria* specimens very closely duplicate the anatomy of *S. sanjuanensis* and, therefore, are easily distinguished from *S. baylorensis*. The German form, however, does appear to exhibit one feature that distinguishes it from the two above species, the primitive possession of a long narrow cultriform process of the parasphenoid. All of the minor differences from *S. sanjuanensis* discussed above may reflect an immature stage of development of the German specimens rather than specific differences. Until more complete specimens of the German form can be studied, it seems best not to create a new species on the basis of one primitive feature. For these reasons the German *Seymouria* MNG 7727 and 8759 are referred to *S. sanjuanensis*.

DISCUSSION

In addition to *Seymouria*, three other tetrapod taxa have been described or identified from the Bromacker locality on the basis of good skeletal remains. Boy and Martens (1991) described a new genus of protorothyridid captorhinomorph, *Thuringothyris mahlendorffae*, whereas other specimens were tentatively identified by Martens (1988, 1989) as amphibians belonging to the families Trematopidae and Limnoscelidae. Also discovered recently but not reported from the Bromacker locality is a skull of a diadectomorph amphibian that is very close to *Diadectes*, if not congeneric, and is presently being studied by the authors. As in the case of *Seymouria*, trematopids, diadectid and limnoscelid diadectomorphs, and captorhinomorphs have not previously been reported, at least not on the basis of substantial evidence, from any other locality in the Rotliegend or its equivalents in France or England. At least two explanations can be offered for the absence of representatives of these taxa elsewhere in the Lower Permian of central and western Europe.

Poor exposures and the long-standing, widely accepted misconception that the red beds of the Upper Rotliegend represent an inhospitable dry climate in which the preservation of vertebrate skeletal remains would have been unlikely have combined to foster a history of little interest in their exploration. This has had the expected result of there being only a very small number of vertebrates collected from the Upper Rotliegend. Alternatively, most investigators have concentrated on the lacustrine grey sediments and black shales of the Lower Rotliegend in which are found such well-known tetrapod localities as Niederhaesslich, Friedrichroda, and various Saar-Nahe sites such as Lebach. These sediments have produced a preponderance of obligatory aquatic amphibians, particularly those of the larval "branchiosaur" amphibians. On the other hand, representatives of a terrestrial or semi-terrestrial fauna preserved as skeletal remains from the Rotliegend and its equivalents (Autunian and Saxonian) in France and England are widely scattered and quite rare. These include the microsaur amphibians *Saxo-*

nerpeton and *Batropetes* (Carroll and Gaskill, 1978; Carroll, 1991), the possible diadectid ?amphibian *Phanerosaurus* (Geinitz and Deichmueller, 1882), the pelycosaur reptiles *Haptodus* (Paton, 1974; Currie, 1979), *Ophiacodon* (Paton, 1974), *Edaphosaurus* (Jaekel, 1911), *Sphenacodon* (Paton, 1974), and *Casea* (Sigogneau-Russell and Russell, 1974), and the questionable araeoscelid diapsid reptile *Kadalsiosaurus* (Credner, 1889). Of the above list, however, only specimens of the pelycosaurs *Haptodus*, *Ophiacodon*, *Sphenacodon*, and *Casea* from France and England were recovered from red-bed deposits.

The Bromacker locality is, therefore, unique among Rotliegend or equivalent deposits in central and western Europe for its high representation of terrestrial or semi-terrestrial vertebrates. This aspect of the assemblage will undoubtedly increase as more skeletal remains from the Bromacker locality are studied. In this regard it is worth noting that trackways from the sandstone units of the Tambach Formation (Pabst, 1896, 1908; Haubold, 1971, 1973; Boy and Fichter, 1988) and other Rotliegend localities indicate a diverse terrestrial tetrapod fauna, including pelycosaurs. Despite the presently limited picture of the Bromacker assemblage, it clearly indicates a very close alliance with those of the Lower Permian red-bed deposits of the Dunkard Group of the eastern United States (Romer, 1952; Berman and Berman, 1975; Olson, 1975) and, particularly, the southwestern United States (Olson and Vaughn, 1970). The apparent explanation for the similarity between the widely separated Lower Permian red-bed tetrapod assemblages of the Bromacker locality and those of the United States is that similar environments are being sampled. This, in turn, would suggest that barriers to faunal interchange between these widely distant regions could not have been strong, though regional differences would be expected.

Although there is no doubt that the Bromacker vertebrate assemblage indicates a Lower Permian horizon for the Tambach Formation of the Upper Rotliegend of the Thuringian Forest in central Germany, the presence of *Seymouria* specimens referable to *S. sanjuanensis* strongly suggests an earliest Permian age of Wolfcampian.

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FRESHWATER MUSSELS (MOLLUSCA: PELECYPODA: UNIONIDAE) OF
TELLICO LAKE: TWELVE YEARS AFTER IMPOUNDMENT OF
THE LITTLE TENNESSEE RIVER

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ABSTRACT

A species survey of freshwater mussels (Pelecypoda: Unionidae) inhabiting Tellico Lake, Monroe and Loudon counties, Tennessee, was carried out from November 1990 to April 1991. Seventy collection stations and an additional 24 km of exposed beach were examined for unionid shells. All specimens encountered were collected and counted. Fourteen native taxa were represented. *Anodonta grandis* is the most abundant and widespread species in the lake; eight others, all silt-tolerant species, are also widely distributed with viable local populations. Based on taxa identified from aboriginal sites along the Little Tennessee River and from recent mussel surveys, 50 unionid species inhabited the river prior to its impoundment in 1979. Only 15 to 18 of these were reported still inhabiting the river in 1972; 12 years after formation of Tellico Lake, only six of those taxa have been found, while eight others previously unrecorded have invaded the lake.

INTRODUCTION

Arising in Rabun County, Georgia, at an elevation of 1000 m, the Little Tennessee River flowed 214 km to its confluence with the Tennessee River. It once flowed freely, cascading over Precambrian and Cambrian sandstones, shale and siltstone in the Blue Ridge physiographic province between the Unaka Mountains of Georgia, North Carolina, and Tennessee to about 53 river km above its confluence with the Tennessee River. About 7 km below that point, the river widened and slowed as it entered the Ridge and Valley province of Ordovician limestone and dolomite at an elevation of just under 250 m, transforming from a montane to a lowland river. This lower 53 km of the Little Tennessee River (now Tellico Lake), from Chilhowee Dam to its confluence with the Tennessee River at Lenoir City, is the section surveyed by us for mussels. Composition of the substrate of this lower 53 km of the Little Tennessee River has been characterized as "... bedrock-boulder, boulder-cobble, sand-gravel, sand and silty sand" (Starnes, 1977: 30).

Molluscan remains recovered and identified from aboriginal habitation sites excavated along the Little Tennessee River prior to its impoundment in 1979 provide evidence of the abundance and variety of species that formerly inhabited the river. At the Toqua site (40MR6), between river km 36.8 and 37.6, Bogan (1987) identified 40 species of mussels. Many of the species represented at the

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Toqua site also were found in archaeological context at other sites such as Martin Farm (40MR20), river km 35.5 (Bogan and Bogan, 1985), and Bat Creek (40LD24) (Schroedl, 1975). In sampling the benthic fauna of the Little Tennessee River for the Tellico Project Environmental Impact Statement, Tennessee Valley Authority (TVA) biologists recorded 22 species of mussels inhabiting the river below Chilhowee Dam (TVA, 1972). Although the thoroughness of the survey is questionable as is the taxonomic allocation of certain species, and the fact that inclusion of two taxa was based on earlier collections (Ortmann, 1918), these pre-impoundment collections indicated that at least 15 to 18 species known prehistorically inhabited the river at the time the Tellico Dam gates were closed.

Impoundment of the Little Tennessee River, from the Tellico Dam at the confluence of the Little Tennessee River and the Tennessee River near Lenoir City (Loudon County) to a point approximately 0.8 km below Chilhowee Dam (Blount/Monroe counties), a distance of approximately 52.8 km, resulted in the formation of Tellico Lake (Fig. 1). The reservoir inundated approximately 5,760 ha (TVA, 1972), including 32 km of the lower Tellico River, a major tributary of the Little Tennessee River. Normal reservoir level at full summer pool is 243.9 km above Mean Sea Level (AMSL); after drawdown in November winter water levels fluctuate between 242.1 and 242.6 km AMSL. As construction of the Tellico Dam neared completion, a canal was excavated to connect the new Tellico Lake with Fort Loudoun Lake (Tennessee River), an 88 km long reservoir resulting from the construction of Fort Loudoun Dam in 1943 by the TVA. This made Tellico Lake and Fort Loudoun Lake essentially one large reservoir. The canal provided direct access for fish from Fort Loudoun Lake to Tellico Lake. As a result fish parasitized with glochidia were probably the primary source of mussel species that invaded Tellico Lake.

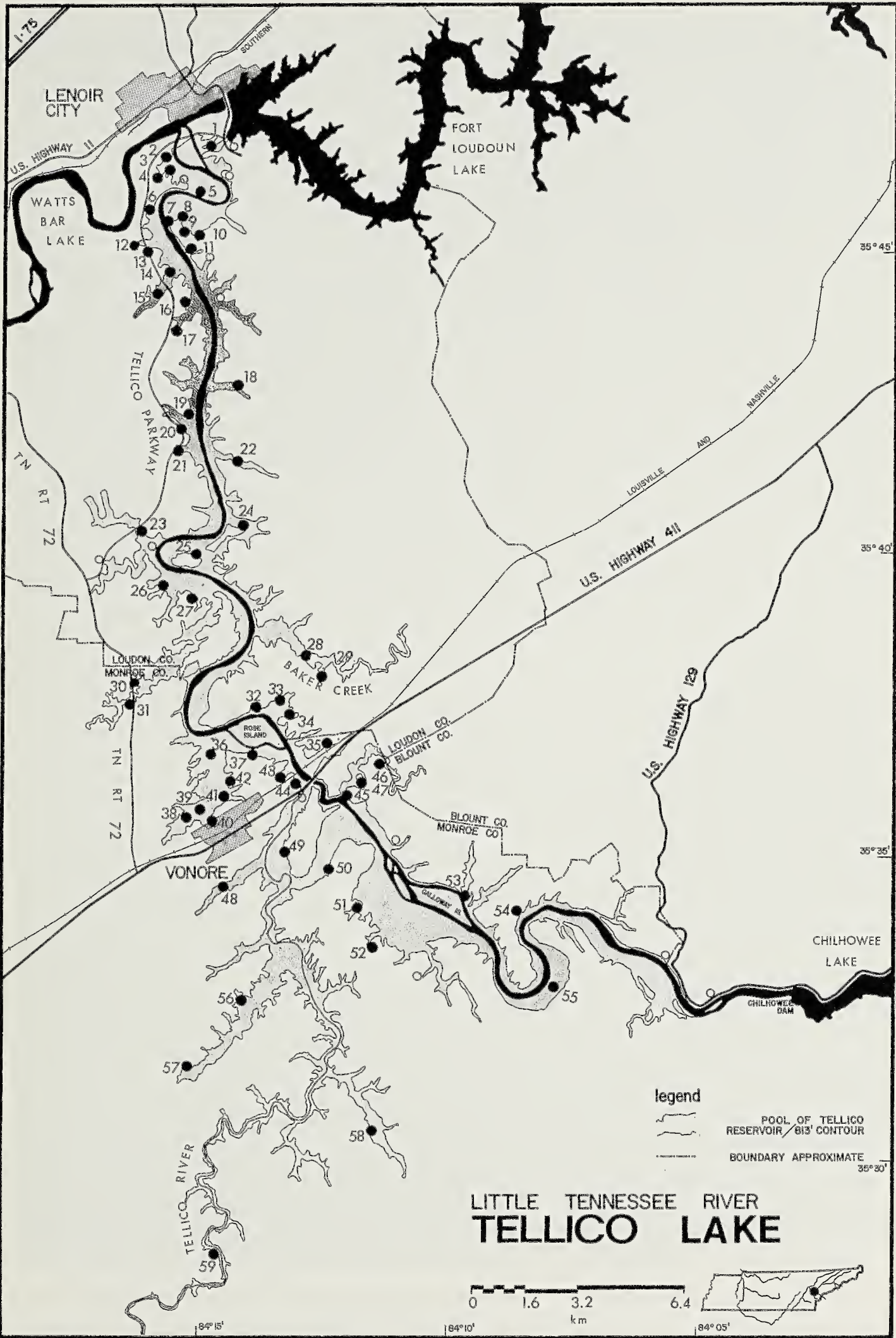
METHODS

Tellico Lake, which has been established for slightly over a decade, provided an opportunity to document changes in the molluscan fauna of a river when it is converted into a reservoir. To assess the distribution and species assemblage of freshwater mussels inhabiting Tellico Lake surveys were conducted following the November drawdown, as the lowered reservoir level (ca. 2 m) resulted in extended stretches of exposed banks, shallow coves (Fig. 2), and beaches surrounding low-lying islands. County and private roads provided access to the reservoir at numerous points along both shorelines. In addition, a 12-foot john boat was used to survey islands and stretches of shoreline inaccessible by road. A minimum of 24 km of shoreline was surveyed by moving slowly parallel to the banks and beaches, searching for shell by visual observation aided by the use of binoculars. In addition to surveying exposed substrate that appeared to be suitable mussel habitat (composites of sand, fine gravel and mud), shale and red clay banks were also scrutinized but with negative results.

Juvenile shells of mussels inhabiting the Tennessee River reservoirs might conceivably be overlooked. However, we demonstrated by recovering 75 juveniles of *T. donaciformis*, a small species that rarely exceeds 40 mm in length, from the exposed beaches of Babe's Island (Watts Bar Lake, Tennessee River km 896.5) in under two hours, that shells of even minute individuals (<15 mm) were easily discernible. Shells were found at 59 of the 70 Tellico Lake collection stations (Table 1).

Collection stations were selected to sample the entire length of the Tellico reservoir, including the islands, embayments, coves and impounded lower stretches of numerous former tributaries of the Little Tennessee River. Shells left by muskrats, *Ondatra zibethica* (Linnaeus, 1766), at feeding stations proved to be a primary source of specimens. These aquatic rodents usually bring mussels to feeding stations such as stumps, overhanging trees, brush piles, riprap, and even silo interiors (see Fig. 2). But

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Fig. 1.—Distribution of collecting stations (solid dots = mussels present, open circles = mussels absent) in the Tellico reservoir, and relationship of original channels of the Little Tennessee and lower Tellico rivers to Tellico Lake.



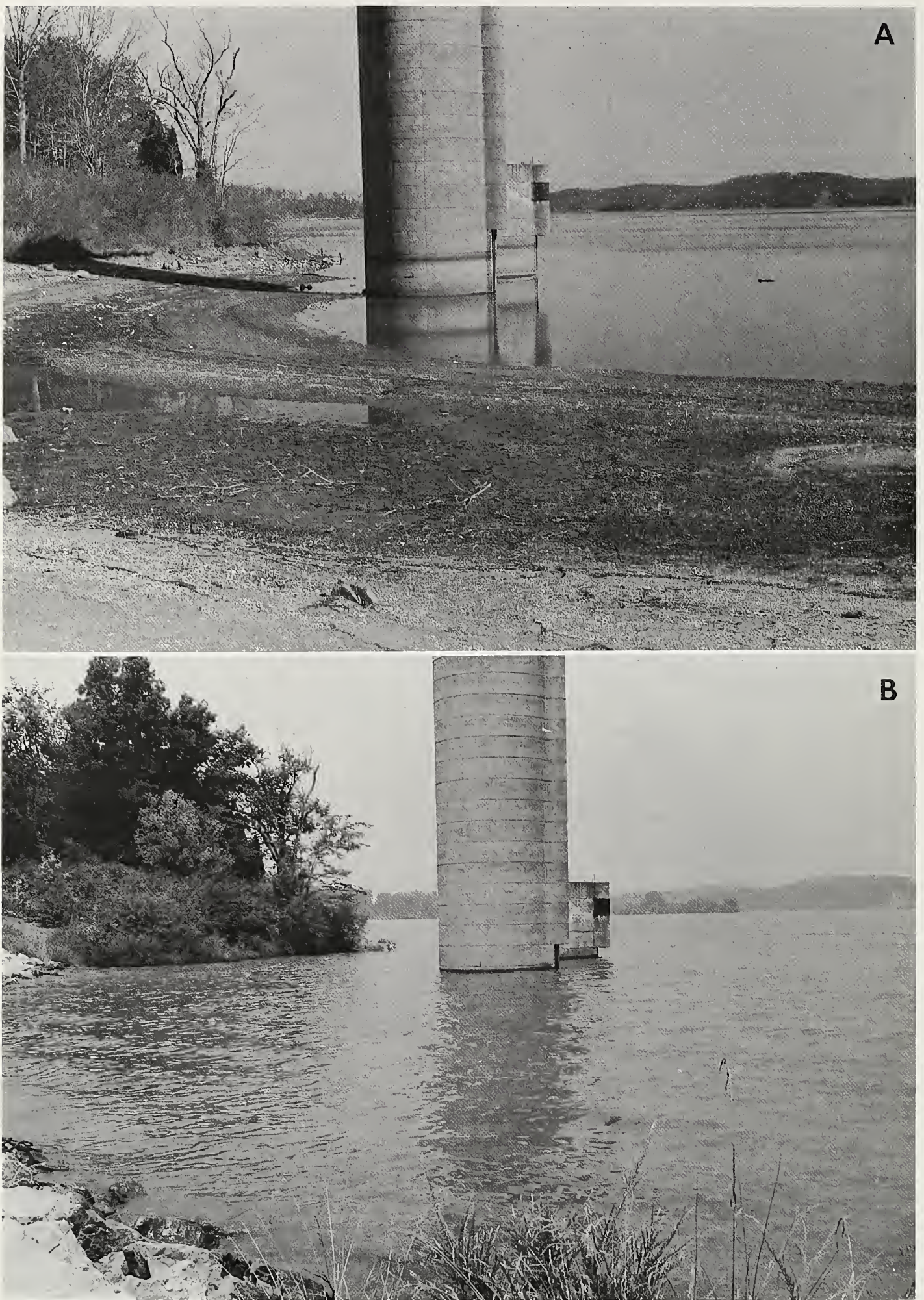


Fig. 2.—Tellico Lake, Loudoun County, Tennessee, Collection Station 6, showing exposed beach and low water level during winter drawdown (A) and summer full pool level (B).

large heavy individuals such as mature *Anodonta grandis* and *Lasmigona complanata*, retrieved as the water receded, were carried into the shallows and eaten there. Collection stations varied in size from an isolated muskrat feeding station to stretches of exposed beach. However, all shells found at each station were collected, counted and recorded. Identifications were made by comparison with specimens in the malacology collections at the Frank H. McClung Museum, University of Tennessee-Knoxville. Because of the discrepancy in the size and/or form (e.g., beach vs riprap) of collection stations, only the presence of the species identified from each is indicated (x) in Table 2.

Voucher specimens of shells obtained during this study were deposited in the Frank H. McClung Museum collections, and voucher specimens of some taxa have been deposited in the Department of Malacology, Academy of Natural Sciences of Philadelphia, and the Section of Invertebrate Zoology, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. Unionid taxonomy used in this study is from Turgeon et al. (1988).

DISCUSSION

Starnes and Bogan (1988) listed 50 unionid taxa for the Little Tennessee River. Sixteen, or 32%, are known only from the archaeological record. Species such as *Elliptio dilatata* (Rafinesque, 1820), *Pleurobema oviforme* (Conrad, 1834), *Fusconaia barnesiana* (Lea, 1838), *Fusconaia subrotunda* (Lea, 1831), *Lampsilis fasciola* Rafinesque, 1820 and *Actinonaias ligamentina* (Lamarck, 1819) inhabited numerous stretches of the river and several of its major tributaries. Favorable habitat consisted of moderate current, riffles and shallow pools and a substrate composed of silt, sand and fine to coarse gravel. Except for the Asian clam and six native unionid taxa, all other mussel species recorded for the Little Tennessee River disappeared before or shortly after impoundment.

Studies comparing the pre-impoundment molluscan fauna of a river with the fauna of the resulting reservoir (Parmalee et al., 1980; Parmalee et al., 1982) have shown that major changes take place as a result of such habitat modification. In a survey of the mussel fauna of a 17.6 km stretch of Fort Loudoun Lake, Isom (1971) found only four native species inhabiting this former section of river. Ortmann (1918) reported around 64 species from the Tennessee River in the general area surveyed by Isom. However, the species reported by Isom (1971) were the result of one day's collecting, so a more extensive survey of the reservoir may have yielded additional species. Nevertheless, the few taxa represented in the survey (Isom, 1971), and Isom's discussion of possible reasons for the absence of other expected species, have a bearing on our analysis of the mussel assemblage extant in Tellico Lake.

Three species of *Anodonta* were encountered during the survey of Tellico Lake. *Anodonta grandis*, primarily the form *A. g. corpulenta* (Cooper, 1834), was the most numerous and widespread of the three. *Anodonta imbecillis* Say, 1829 is also well established throughout Tellico Lake, but populations appear to be more localized than those of *A. grandis*, and occur primarily in shallow embayments and coves with substrates of mud (silt) and fine sand. Populations of *Anodonta suborbiculata* Say, 1831, like those of *A. imbecillis*, are localized in the same type of habitat but are more limited in distribution. Specimens of *A. suborbiculata* were encountered at only nine of 70 collection stations. With the exception of Baker Creek (Station 29), all were found in the lower stretches of the reservoir within 12.5 km of Tellico Dam.

Isom (1971) first recorded *A. corpulenta* (= *A. grandis*) and *A. imbecillis* from Fort Loudoun Lake, and first reported extensive populations of *A. grandis*, *A. suborbiculata*, and *Lasmigona complanata* (all new distribution records) in Chickamauga Reservoir (Isom, 1969). Except for one specimen of *A. imbecillis* from Savannah, Tennessee, van der Schalie (1939) reported no other species of *Ano-*

Table 1.—*Collection Station number and location on Tellico Lake, with approximate Little Tennessee River km of each. See Fig. 1.*

Collection station number and location	Approximate Little Tennessee River km
1. Tellico Dam Rec. Area	1.6
2. Saddle Dam 1 cove N	0.8
3. Rock Island, Saddle Dam 1 cove	0.8
4. Saddle Dam 1 cove S	0.8
5. Hall Bend Island	4.0
6. Silos, Tellico Parkway	5.4
7. Jackson Bend NW	4.5
8. Jackson Bend NE	5.6
9. Jackson Bend SW	4.2
10. International Harbor	3.8
11. Wyly Cemetery	6.7
12. Impounded pond at Poplar Springs	5.9
13. Poplar Springs Rec. Area	6.1
14. Island south of Poplar Springs	6.2
15. Bay north of Davis Cemetery	7.2
16. North of Davis Cemetery	8.2
17. Davis Cemetery	8.5
18. Axley Cemetery	10.9
19. Tellico Village Yacht Club	12.0
20. Tellico Village town houses	12.5
21. Tellico Village Visitors Center	13.0
22. Sinking Creek	12.5
23. Clear Creek, Tellico Parkway	17.9
24. Lotterdale Cove Rec. Area	14.9
25. Jackson Bend island	18.6
26. Russell Cemetery	18.4
27. High Top	19.0
28. Baker Creek at bridge	21.8
29. Baker Creek S of bridge	21.8
30. Cove along TN Route 72	19.0
31. Bat Creek	19.0
32. Bay just north of Rose Island	27.8
33. Rose Island bay N	28.2
34. Rose Island bay S	28.5
35. Beach North of railroad	28.8
36. Mouth of Island Creek	26.6
37. Bay W of railroad	30.1
38. Island NW of Vonore	26.6
39. Island N of Vonore	26.6
40. Vonore Beach	26.6
41. Island Creek ENE of Vonore	26.4
42. East bank of Vonore bay	26.6
43. Embayment N of railroad	30.1
44. Bay S of railroad	30.1
45. Mouth of Ninemile Creek	32.0
46. Ninemile Creek at TN Route 72	32.0
47. Ninemile Creek at marina	32.0
48. Fourmile Creek	30.4
49. Fort Loudoun State Historic Area	30.4
50. Toqua Cemetery	33.3
51. Toqua Rec. Area N	34.9
52. Toqua Rec. Area S	35.5
53. Smoky Branch Rec. Area	36.8
54. Choata Wildlife Refuge Unit	44.2
55. Tanasi Historic Site	41.6

Table 1.—Continued.

Collection station number and location	Approximate Little Tennessee River km
56. Notchy Creek Rec. Area	30.4
57. Notchy Creek embayment S	30.4
58. Ballplay embayment	30.4
59. Sloan Bridge	30.4

donta in collections (18 localities) from the lower Tennessee River between the confluence of the Hiwassee River, Meigs County, Tennessee, and Paducah, Kentucky. Impoundment of the Tennessee River and its major tributaries such as the Little Tennessee River has reduced in number or eliminated many species, brought about the colonization of shallows by others (e.g., *Anodonta*), and resulted in the establishment of species unreported prior to impoundment (Isom, 1969).

Elliptio crassidens was known from the Little Tennessee River prior to impoundment, and Parmalee and Klippel (1984) reported it from an unimpounded stretch of the Tellico River (Nars Ford, Tellico River km 34.4–35.2), approximately 4 km upstream from the Tellico Reservoir. In this survey only one specimen of *E. crassidens* was recovered, a juvenile ($59.0 \times 35.5 \times 24.0$ mm) at Collection Station 6. It is doubtful whether the original population(s) of this mussel in the Little Tennessee River and the Tellico River (only five specimens recovered during numerous collecting trips in 1982 and 1983) survive. Although mature specimens of *E. crassidens* were found during TVA mussel surveys of the Chickamauga and Watts Bar reservoirs, no juveniles were found (S. A. Ahlstedt, personal communication, 1991). It is doubtful that *E. crassidens* would become established in a lake or river embayment totally lacking current. A single mature specimen of *Truncilla donaciformis* was found at Collection Station 21, and three specimens of *T. truncata* (Rafinesque, 1820), one juvenile and two adults, were found (probably taken by muskrats) at Collection Stations 4 and 20. It has been shown (Klippel and Parmalee, 1979) that *T. truncata* can develop reproductively viable populations in a lake environment. Isom (1971) collected a single specimen of *T. truncata* in Fort Loudoun Lake, but noted that it was present in the Tennessee River prior to impoundment. Starnes and Bogan (1988) did not record it as part of the unionid fauna of the Little Tennessee River.

Only three small local populations of *Toxolasma parvus* (Collection Stations 29, 30 and 56) and a single individual (Collection Station 19) were encountered during the survey. The species had not been recorded as occurring in the Little Tennessee River. Once established, *T. parvus* can become numerous in shallow, quiet embayments and coves with substrates composed of mud and silt. Such habitat conditions abound in Tellico Lake, and in time this species may become more numerous and widespread. *Lasmigona complanata*, another taxon previously unreported from the Little Tennessee River, has now become well established and is locally common and widely distributed throughout Tellico Lake. It, like all species presently occurring in the reservoir with viable populations, is silt tolerant and thrives in shallow coves and embayments.

Three species, *Potamilus ohiensis* (Rafinesque, 1820), *Potamilus alatus* (Say, 1817), and *Leptodea fragilis* (Rafinesque, 1820) were part of the Little Tennessee River unionid assemblage (Starnes and Bogan, 1988), but their former relative abundance is unknown. Of the three, *P. ohiensis* is the most common and widely

Table 3.—Relative abundance of freshwater mussels as indicated by muskrat predation during December 1990–March 1991 at Collection Station 46. Area sampled consisted of a 67.5 m stretch of beach/shallows near the former confluence of Ninemile Creek and the Little Tennessee River.

Species	Date collected			
	4 Jan.	3 Feb.	2 Mar.	5 Apr.
<i>Anodonta grandis</i>	6	1	2	5
<i>Anodonta imbecillis</i>	2	1	1	1
<i>Lasmigona complanata</i>	12	11	7	4
<i>Leptodea fragilis</i>	1	—	1	—
<i>Obliquaria reflexa</i>	181	106	59	47
<i>Potamilus alatus</i>	1	1	1	2
<i>Potamilus ohiensis</i>	12	22	20	19
Totals	215	142	91	78

distributed in Tellico Lake, followed by *P. alatus* (found at 18 collection stations) and *L. fragilis* (12 collection stations). These species often become abundant in shallow river embayments and lakes, and in all probability all three are considerably more numerous in Tellico Lake than they were in the Little Tennessee River.

Obliquaria reflexa Rafinesque, 1820, a species typical of medium-sized to large rivers, can adapt to and flourish in lake environments. In the initial study of the unionids of Lake Springfield in central Illinois (Parmalee, 1955), this species was not encountered, but approximately 20 years later it was second in abundance only to *Quadrula quadrula* (Rafinesque, 1820) (Klippel and Parmalee, 1979). *Obliquaria reflexa* occurs throughout Tellico Lake and is locally abundant. Age estimates of large mature specimens, based on rest lines in the periostracum, suggest that this mussel became established in the reservoir within two years of filling. Isom (1971) did not encounter this mussel during his survey of Fort Loudoun Lake, but it has been observed and collected there by us and others during the past four to five years. Fort Loudoun Lake is probably the source from which the Tellico Lake populations derived.

From January 4 through April 5, 1991, shells left by muskrats were collected among a 67.5 m stretch of beach and shallows at Ninemile Creek (Collection Station 46). The collections resulted from muskrat predation over approximately a four-month period as the initial collection included individuals from December and possibly late November, 1990. A total of 526 specimens was recovered (Table 3), of which 393 (75%) were *O. reflexa*. A decline in the number of mussels taken by muskrats from mid-winter to early spring is apparent in the case of *O. reflexa*. Probably heavy predation on this bed was a contributing factor in the decline of individuals of at least this species during the winter.

The distribution of *Quadrula pustulosa* (Lea, 1831) appears to be restricted to the lower portion of the reservoir near Tellico Dam. Only four specimens were recovered (Collection Stations 1, 9, 10). Although the two largest individuals exhibit eight distinct rest lines on the periostracum, suggesting their presence three to four years after formation of the lake, a viable population has not become established.

Although *Q. pustulosa* appears to be relatively uncommon in upper Watts Bar Lake below Fort Loudoun Dam (Tennessee River (TR) km 944) (Ahlstedt, 1989), it is locally abundant in lower sections of the reservoir. For example, a collection

from an approximately 180 m long by 18 m wide stretch of beach at Fooshee Pass Recreation Area, Meigs County (TR km 861), included 545 specimens representing five species. Eighty-three percent were *Q. pustulosa*. Of the six species of fish recorded by Fuller (1974) as hosts for the glochidia of *Q. pustulosa*, at least four (channel catfish, *Ictalurus punctatus*; black bullhead, *Ictalurus melas*; flathead catfish, *Pylodictus olivaris*; white crappie, *Pomoxis annularis*) are common throughout the reservoir. Why viable populations of *Q. pustulosa* have failed to become established in the Tellico and Fort Loudoun reservoirs is unknown.

Villosa vanuxemensis was represented in the Tellico Lake collection by a single mature ($61.0 \times 35.2 \times 31.0$ mm) relict female found on the beach at Collection Station 13. Prior to impoundment this area would have been adjacent to Poplar Springs, a small tributary creek of the Little Tennessee River. This mussel is characteristic of small creeks and headwaters of larger streams in eastern Tennessee and probably inhabited the small tributaries of the Little Tennessee River prior to impoundment. Inadvertently, it was not listed by Starnes and Bogan (1988) as a component of the Little Tennessee River mussel assemblage. Parmalee and Klippel (1984) found that *V. vanuxemensis* was the most abundant mussel in the Tellico River, the major tributary of the Little Tennessee River.

In recent years numerous studies on mussel species diversity and abundance as they relate to potential commercial harvesting and existing ecological conditions (Williams, 1969; Yokley, 1972; Gooch et al., 1979), causes of mortality (Neves, 1987), the location and protection of rare and endangered taxa, and the impact of proposed industrial development (Ahlstedt, 1989) have appeared. Such investigations are essential if freshwater mussels in the Tennessee River, and in other rivers and lakes, are to be protected. In the past, molluscan faunas occurring in newly formed reservoirs, and those which existed in the free-flowing Tennessee River prior to impoundment, often were not evaluated or compared until decades later. Moreover, only limited stretches or local areas, such as Muscle Shoals, Alabama (Stansbery, 1964), have been monitored in detail. Tellico Lake, however, provides an opportunity to compare the mussel assemblage of the Little Tennessee River with one that has invaded and is becoming established in the recently formed reservoir.

The invasion and establishment of mussel taxa in Tellico Lake reflects a pattern typical of other well-established reservoirs in the Tennessee River system. With few exceptions, mussel species that flourished in shoals and riffles of the free-flowing Tennessee River disappeared with impoundment, or surviving taxa were reduced to non-reproducing relict individuals. Although most Tennessee River reservoirs retain strong currents in the old channels and below the dams, constant change in rates of flow and depth, insufficient dissolved oxygen, and continuing deposition of sediment have adversely affected mussel reproduction and actual survival of species (van der Schalie, 1938; Isom, 1969, 1971).

Extensive shallows (<1.5 m depths) along beaches in coves and embayments lacking current presently provide the most suitable mussel habitat and support the greatest number of individuals and taxa in Tellico Lake. Bank run-off and wave action cause erosion that results in a substrate mixture of sand, mud and fine gravel in these shallow areas. Nine of the 14 mussel species inhabiting the reservoir are silt tolerant and typically reach greatest abundance in such habitats. The occurrence of species requiring moderate to strong current and a stable substrate would not be expected in a lake environment, yet a few such as *Obliquaria reflexa* can adapt and thrive in lakes. Recovery of only one single juvenile specimen

of *Elliptio crassidens* from Tellico Lake suggests that this species, which is locally common in the main channel of the Tennessee River, failed to become established in this reservoir.

SUMMARY

Collections of freshwater mussels made during the period November, 1990, through March, 1991, in Tellico Lake, Loudon and Monroe counties, Tennessee, included specimens of 14 native unionid taxa and the Asian clam, *Corbicula fluminea*. The diverse assemblage of naiad species (50) once inhabiting the Little Tennessee River has been reduced in Tellico Lake to six taxa (*Anodonta grandis*, *Elliptio crassidens*, *Quadrula pustulosa*, *Leptodea fragilis*, *Potamilus alatus*, and *Potamilus ohioensis*). Eight species previously unreported from the river and assumed to be of recent origin include *Anodonta imbecillis*, *Anodonta suborbiculata*, *Lasmigona complanata*, *Obliquaria reflexa*, *Toxolasma parvus*, *Truncilla donaciformis*, *Truncilla truncata*, and *Villosa vanuxemensis*. The latter three species, as well as *Q. pustulosa* and *E. crassidens*, were each represented by fewer than six specimens. The paucity of individuals of these five taxa suggests the occasional establishment of one or a few individuals from parasitized fish, or in the case of *V. vanuxemensis* a possible pre-impoundment relict for which this reservoir lacks suitable habitat for establishment of viable populations. An abundance of shallow coves and embayments characterized by a sand/mud/silt substrate in Tellico Lake have allowed the establishment and rapid increase of several species of *Anodonta* and *Potamilus* throughout the reservoir.

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REVIEWS

AUSTRALIAN SNAKES: A NATURAL HISTORY. Richard Shine. 1991. Reed Books Pty Ltd., Balgowlah, NSW, Australia (distributed in the United States by Cornell University Press, Ithaca, NY 14850). 223 p. \$34.95. ISBN 0-7301-0349-8.

I have been collecting illustrated popular books on amphibians and reptiles for about 40 years. From my long-term perspective I have tracked availability and quality (and unfortunately price) of such books as they have followed a steep trajectory. Lately in this explosion of literature Australian publishers have emerged as leaders in the production of high-quality popular herpetological books. "Australian Snakes" is at the peak of the curve, and sets a standard that will be hard to surpass.

"Australian Snakes" should not be viewed as just a book about Australian snakes, although most of the photographs and much of the specific information relate to the peculiarly Australian snake fauna. The terrestrial snakes of that continent derive from a few (three or four) basic stocks, which radiated during long isolation. Seen against the world diversity of snakes the Australian fauna is decidedly depauperate. Therefore to attempt a general work on snake biology using primarily Australian examples would seem an impossible task. But Dr. Shine, who probably knows Australian snakes better than anyone, was equal to the challenge.

The book is admirably organized. The eight chapters include: Anatomy of a Snake; The Evolution of Snakes; Where Snakes Live; The Behavior of Snakes; Snake Life Histories; What Snakes Eat; and Snakes and Humans. The first two chapters are excellent accounts. They can be recommended as general introductions useful on almost any level, as they go beyond the purely Australian focus. Each of the chapters on snake biology is a masterful blend of basic principles, explanations and examples of the principles, and observations and anecdotes. Often the research of Dr. Shine and his students and colleagues provides the anecdotes, which gives the writing style an engaging personal touch. It makes what could be dry subject matter read like a storybook. An amazing amount of original data, mostly from Dr. Shine's research, is presented. Most of these data are summarized in clever, informative graphics.

The illustrations are among the best features of a very good book. Nearly all of the photographs show snakes actually doing something; often something extremely interesting. Each photograph truly "tells a story," and those in the chapter "Snakes and Humans" in particular tell cautionary tales of human frailty and misplaced trust. Numerous photos of Dr. Shine and his students in the field add greatly to the information content of the book, and completely de-mystify field research on wild snake populations. The quality of the color reproductions is excellent, as is the typography throughout the book.

A tabular summary of data on the biology of Australian snakes arranged by species, and a carefully-selected bibliography of additional references are potentially the most useful sections of the book.

Finally, I must reiterate and emphasize a point made previously: this is not just a pretty picture book, nor is it just a book about Australian snakes, although

it certainly is both of those things. "Australian Snakes" provides a concise, thorough, authoritative and readable introduction to the biology of snakes. I recommend it to anyone who wants to understand basic snake ecology, and it should be required reading for students considering field work on snakes.

C. J. MCCOY, *Curator, Section of Amphibians and Reptiles.*

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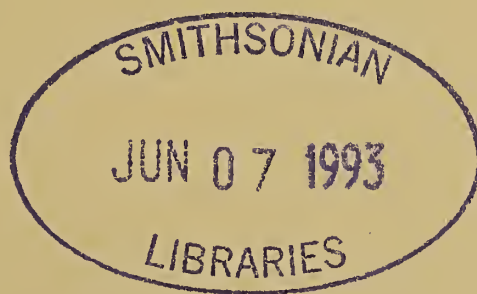
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CERAMIC REMAINS FROM CARL V. HARTMAN'S 1903
EXCAVATIONS AT LAS HUACAS CEMETERY, COSTA RICAMICHAEL J. HECKENBERGER¹

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ABSTRACT

A descriptive analysis was conducted on 15 ceramic artifacts excavated in 1903 from the Las Huacas cemetery site on the Nicoya Peninsula of Costa Rica by Carl V. Hartman, then Curator of Archaeology and Ethnology at the Carnegie Museum of Natural History. The results are presented here together with a brief discussion of site and burial context at Las Huacas. An additional 59 small globular vessels excavated by workmen from Las Huacas during Hartman's expedition are discussed in less detail. The data recovered through Hartman's investigations at the site are still among a relatively small body of data from well-excavated cemetery context in the Nicoya region of northwestern Costa Rica. Much of the material from the site remains to be properly described. In particular, the ceramic remains, which have been the primary means of assessing the antiquity of the site, have not been adequately reported in the literature. The data presented here are correlated with other sites from the region to place Las Huacas in the context of more recent research conducted in the Nicoya area since Hartman's time.

INTRODUCTION

In 1903, Carl V. Hartman began excavations at the Las Huacas cemetery site on the Nicoya Peninsula of northwestern Costa Rica (although Hartman used the spelling Las Guacas, it has become conventional to spell it Las Huacas). This expedition was sponsored by the Carnegie Museum of Natural History (CMNH) where Hartman had become Curator of Archaeology and Ethnology that same year. During his fieldwork in northwestern Costa Rica, Hartman also purchased several large collections from the site and nearby areas. The materials recovered from Hartman's fieldwork and those portions of the purchased collections directly attributed to Las Huacas constitute one of the largest assemblages of artifactual remains from a single Costa Rican archaeological site and are among the only such data sets from excavated cemetery context on the Nicoya Peninsula. As such, this assemblage offers a unique perspective on regional prehistory in northwestern Costa Rica and surrounding areas.

Of particular significance within these collections are the materials actually excavated by Hartman. The exacting and systematic methods employed by Hartman in his excavations provide adequate documentation of his finds, even by today's standards (Rowe, 1959; Skirboll, 1984a; Willey and Sabloff, 1980). Provenience data recorded by Hartman have enabled later researchers to reconstruct the contextual relationships of many of the artifacts and cultural features and thus assess the significance of the materials to local and regional prehistory (Fonseca

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and Richardson, 1978; Fonseca and Scaglion, 1978; Ohlsson, 1991; Skirboll, 1981). Much of the Costa Rican material obtained by Hartman for CMNH remains to be thoroughly analyzed and described, however. The ceramics from Hartman's excavations at Las Huacas, the focus of the present paper, are among those materials which are only partially reported.

Archaeological remains from Las Huacas and surrounding areas curated at CMNH are divided into three separate assemblages. These are: the Hartman collection (excavated during Hartman's expedition), the Velasco I collection (artifacts from Las Huacas purchased from Father José Maria Velasco by Hartman), and the Velasco II collection (artifacts from Las Huacas and vicinity purchased by Hartman from Velasco) (Fonseca and Scaglion, 1978). The Hartman collection is further subdivided here into the Hartman I subcollection (HI), excavated by Hartman, and the Hartman II subcollection (HII), excavated by workmen hired by Hartman during his expedition. The present discussion focuses primarily on the ceramic remains from the Hartman I subcollection due to their recovery from recorded burial context. An additional 59 ceramic vessels from the Hartman II subcollection are described for comparison.

SITE SETTING AND CULTURAL CONTEXT

The Las Huacas cemetery site, in the province of Guanacaste, Costa Rica, lies on a forest-covered mountain ridge (averaging 600–800 m a.s.l. in elevation) which runs along the center of the Nicoya Peninsula. Las Huacas is situated between the headwaters of two prominent rivers, the Morote River draining to the east into the Gulf of Nicoya and the Nosara River draining west into the Pacific Ocean (Fig. 1). The cemetery was several acres in extent and located on a level portion of the mountain pass *La Quebrada de Las Guacas*, separating the *Cordillera de Santa Rita* and the *Cordillera de Canillas*, about 18 km southwest of the town of Nicoya (Hartman, 1907:14).

Las Huacas, and the entire Nicoya Peninsula, fall within the "Greater Nicoya Archaeological Subarea," an area that extends from the Gulf of Fonseca in Pacific Nicaragua in the north to the Nicoya Peninsula (Lange, 1984). Broad artifactual similarities exist across the Greater Nicoya Subarea; however, important differences, especially with regard to ceramic styles and other artifact types, allow for distinction between a northern sector and a southern sector (Lange, 1984; Lange et al., 1984; Lange et al., 1992). The materials recovered by Hartman from Las Huacas conform well to ceramic types considered characteristic of the southern sector (consisting of northwestern Costa Rica including the entire Nicoya Peninsula). Most notably, Guinea Incised and Marbella Zoned Impressed Punctate types are well represented in the Las Huacas collections. These ceramic types and others from Las Huacas are for the most part related to the Zoned Bichrome period of regional prehistory. This period is generally considered to span from ca. 600 B.C.–A.D. 500. Temporal periods have been defined for the Nicoya Peninsula area based largely on several ceramic sequences for the Tempisque River valley, the Pacific coastal area between Tamarindo Bay and the Nosara River valley, and the Bay of Culebra (Fig. 2). The Las Huacas material most closely corresponds to the ceramic sequences described for the Tempisque Valley (Baudez, 1967) and the Bay of Tamarindo/Nosara Valley (Sweeney, 1975; Lange et al., 1976), but also corresponds to other Greater Nicoya southern sequences from the Bay of Culebra and the Santa Elena Peninsula farther to the north (Lange, 1984). The sequence of the Tempisque Valley is used here to classify the Las

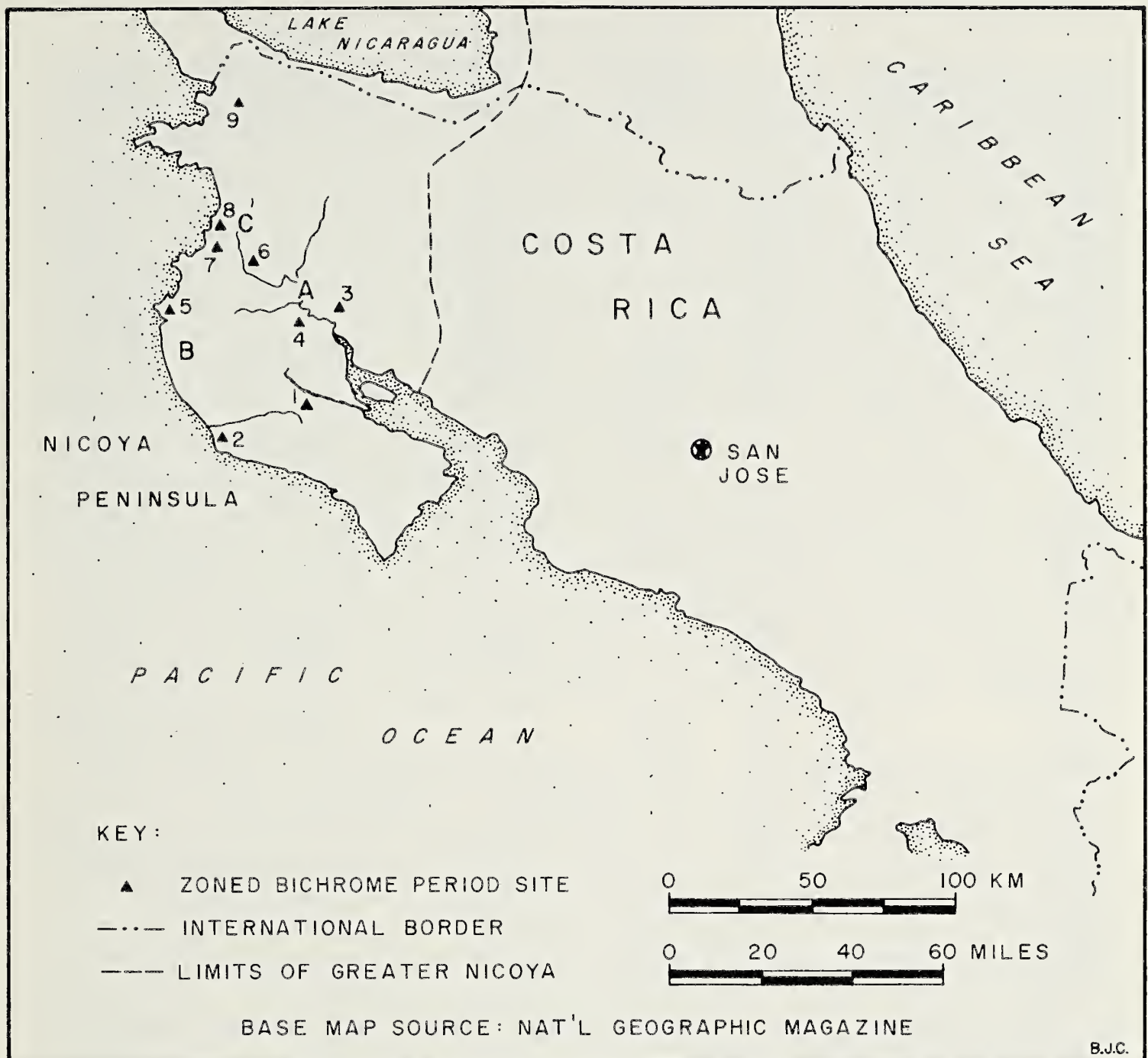


Fig. 1.—Map of Costa Rica showing the limits of the Greater Nicoya archaeological subarea and the locations of select Zoned Bichrome period sites referenced in the text, including: (1) Las Huacas, (2) Nosara, (3) El Carmen, (4) Bolson, (5) Matapalo, (6) Hacienda Tempisque, (7) Vidor, (8) Nacascolo, and (9) Las Pilas. Note that the designation “A” refers to the general location of the Tempisque River Valley sequence from Fig. 2; “B” is the Matapalo, Tamarindo, and Nosara sequence; and “C” is the Bay of Culebra sequence.

Huacas ceramics, but the phases of the Tempisque Valley correlate almost exactly with the phases of other sequences from southern Greater Nicoya.

The inception of the Zoned Bichrome period (Period IV in the revised Central American chronology [SAR; *see* Lange and Stone, 1984]) also marks the appearance of pottery in the region, with a generally accepted date of 600–500 B.C. Earlier ceramics (Schettel Incised) are known for the Loma B phase, dated to ca. 800 B.C. at the Vidor site in Bay of Culebra (Lange, 1980) and adjacent areas including the Guanacaste–San Carlos corridor (Norr, 1986) and Rivas Isthmus region (Haberland, 1992; Healy, 1980). Similar ceramics occur even earlier in the Arenal area adjacent to Greater Nicoya in the central highlands of Costa Rica

Date	SAR Period		Regional Period	Tempisque River Valley	Matapalo, Tamarindo and Nosara	Bay of Culebra
1500						Ruiz
1400			Late			
1300	VI	Polychrome Periods		Bebedero		Iquanita
1200						
1100				(B)	(B)	Monte de Barco
1000				Palo Blanco		
900					Tamarindo	
800	V		Middle	(A)	(A)	Panamá
700						
600			Early	San Bosco*	Matapalo	Culebra
500						
400				Ciruelas*	Las Minas	Mata de Uva
300			Late			
200						
AD 100						
0		Zoned Bichrome Period		Catalina*	Monte Fresco	Orso
100 BC						
200	IV					
300			Middle			
400						
500						
600						
700						Loma B
800						
900						
1000			Early			

Fig. 2.—Chronological chart for archaeological phases from the Nicoya Peninsula (Note: asterisk denotes phases represented at Las Huacas).

(Sheets et al., 1991). There is no evidence of an early Zoned Bichrome (ca. 1000/800–300 B.C.) usage of the Las Huacas cemetery.

The Las Huacas ceramics are primarily related to types of the middle (ca. 300 B.C.–A.D. 300) and late (ca. A.D. 300–500) Zoned Bichrome period, designated as the Catalina and Ciruelas phases respectively in the Tempisque sequence. Zoned Bichrome period ceramics from Greater Nicoya are generally characterized by several distinctive techniques, including: “(1) incising, engraving, ridging, and punctating; generally these outline or demarcate black, red, or unpainted zones; (2) Bichrome painting, particularly black on a red base slip; (3) multiple brush and/or resist (negative) painting” (Healy, 1980:300). Galo polychrome ceramics of the Early Polychrome period, ca. A.D. 500–800, demonstrate a later usage of the cemetery. Fonseca and Scaglione (1978:284) estimate cemetery duration from ca. A.D. 180–525. Although the cemetery may have been in use for a longer period, available ceramic evidence from the site supports this estimate as the primary period of cemetery usage.

BURIAL FEATURES

Hartman first visited Las Huacas in 1896 but could not obtain permission to conduct excavations. He returned to the Nicoya Peninsula in 1903, during his first year as CMNH curator, and conducted four weeks of excavations at the site. Hartman excavated at least 17 burial features in a largely undisturbed portion of the site (Fig. 3; *see* Hartman, 1907:plate XLVII for greater detail). Other burial features at the site were simultaneously excavated by hired workmen, but were not described or mapped by Hartman. He does state, however, that “all the burials . . . appeared to be of the same general character [as those Hartman excavated himself], but the burial-ground at this part being deeper, the fragments of skeletons appeared in two layers . . .” (Hartman, 1907:32). In the only description of an actual burial from the workmen’s excavations, Hartman (1907:32) noted that “not less than fourteen metates . . . were found almost in one heap . . . covering the fragments of several skeletons.”

During his own excavations, “numerous pieces of broken pottery . . . [were] met with close to the surface” (Hartman, 1907:14). This upper stratum (stratum III) consisted of a layer of black humus about 50 cm in thickness in which “numerous pieces of red and black potsherds” were recovered (Hartman, 1907:15). It is not certain if these materials relate to domestic activities carried out at the site during or after cemetery usage, although the co-occurrence of domestic and cemetery remains in single sites is known from other portions of Greater Nicoya (Lange, 1984).

Below stratum III, a “layer of red clay was met . . . [with] a thickness of from one to one and a half meters . . . [which] rested upon a layer of yellowish conglomerate of rather hard consistency” (Hartman, 1907:15). These two strata are herein designated as stratum II (red clay layer) and stratum I (yellowish conglomerate). The burial pits were recognized in stratum I and it was “through its [the burial pit] looser consistency” (Hartman, 1907:15) that he was able to determine the location and form of graves. Hartman (1907:15) states that “In this substratum [stratum I], . . . the Indians had hollowed out pits or cavities, more or less oval or circular, and in these had placed the bodies of their dead” While not explicitly stated by Hartman it is assumed here that the depths given for individual burial pits refer to their depth below the ground surface.

Fonseca and Scaglione (1978:297) have suggested that burials excavated by Hartman occurred in two levels, which they indicate may reflect temporal variation. The present analysis suggests that this distinction may be arbitrary and not reflective of temporal differences. Most pits extended deeper than 1.5 m, typically to maximum depths between 1.8–2.4 m (Table 1).

Hartman himself excavated 16 intact burial features and one disturbed feature (probably two or more mixed features). Hartman’s (1907:16–32) descriptions of these burials are summarized here in Table 1. Several aspects of the burial pits at Las Huacas merit further discussion. First, given the detail and accuracy of Hartman’s 1907 site map, it is reasonable to assume that his renderings of skeletal remains are at least roughly accurate with regard to number of individuals (estimated by number of skulls) and placement of bones within burial pits. The size of the burial pits and Hartman’s renderings of the skeletal remains indicate that no extended burials were encountered and it appears, in fact, that no primary burials were encountered at all. This cannot be asserted with certainty since the skeletal remains from many burials were fragmentary. Hartman (1907:16) does

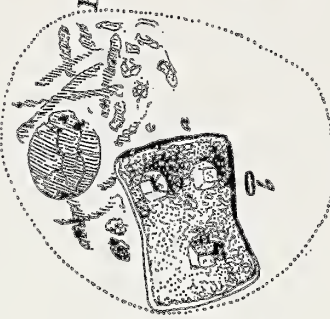
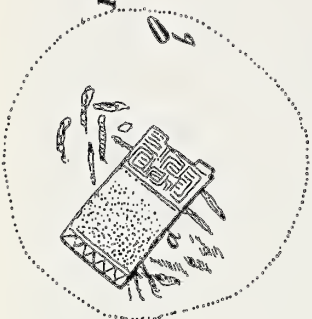
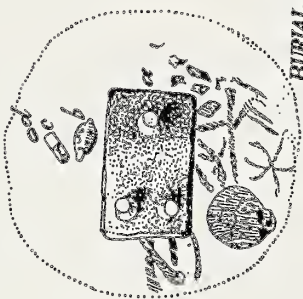
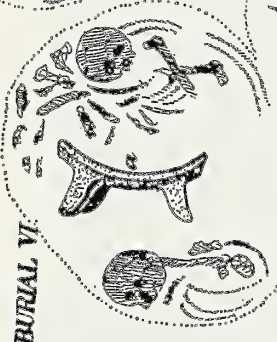
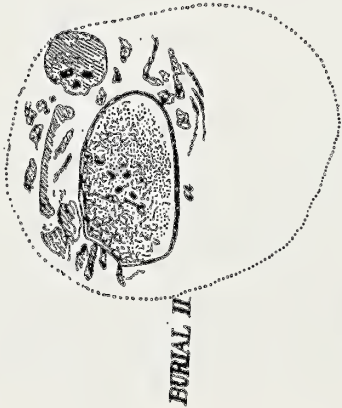
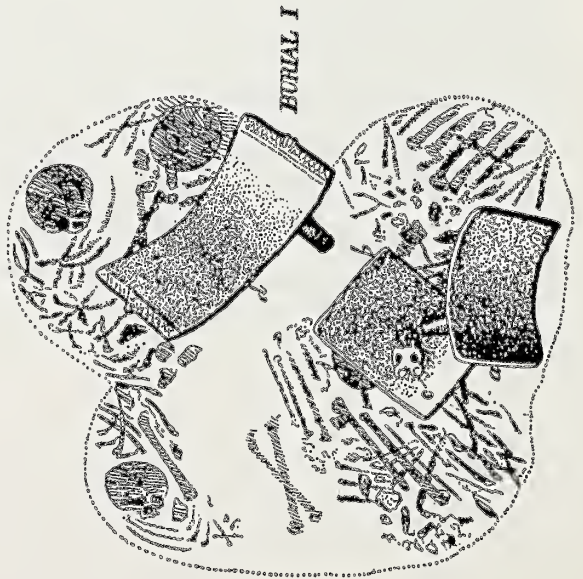
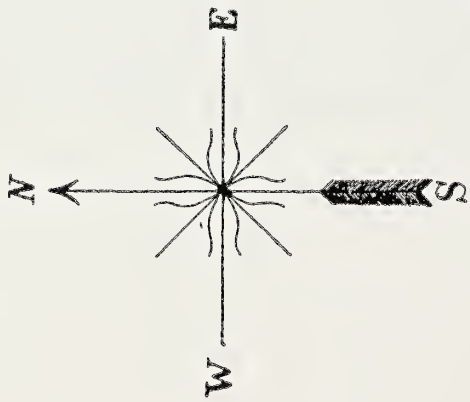


Table 1.—*General attributes of burial features at Las Huacas. Asterisk denotes possible intersecting burials.*

Burial number	Shape	Maximum diameter (m)	Maximum depth (m)	Number of individuals	Artifact inclusions
I*	irregular	1.5	2.1	5	3 metates figurine
II	circular/ovoid	1.0	1.5	1	metate
III	circular	1.0	2.0–2.4	2	none
IV	ovoid	1.1	2.2	1	metate
V	circular/ovoid	1.0	2.0–2.4	2	none
VI	circular	0.8	2.2	2	metate
VII	circular	1.0	2.0	1	slate fragment metate leg pottery fragments
VIII*	irregular	1.5	2.0–2.4	3	3 metates 2 amulets figurine pestle
IX	circular	1.0	1.8	1	metate ocarina amulet polishing stone
X	circular	1.5	NA	NA	none
XI	circular	1.0	2.0	1	metate celt
XII	circular/ovoid	1.0	1.5	1	metate polishing stone
XIII	circular	1.15	1.0	1	small vessel 2 polishing stones
XIV	circular	1.25	1.2	1	none
XV	ovoid	2.0	1.35–2.3	4	small vessel 5 beads
XVI	ovoid	1.0	1.9	1	metate 3 amulets 2 beads
XVII*	NA	NA	NA	3+	3 metates 12 amulets 4 celts 3 beads 2 mace-heads barkscraper 3 polishing stones 7 small vessels ocarina figurine

state in reference to Burial I that: “The bones were placed in heaps close to the skulls, showing here, as in every other part of the cemetery, the prevalence of the method of bunched burials.”

Several multiple burials (I, III, V, VI, VIII, X, XV, and possibly XVII) were excavated. Some of these (e.g., I, VIII), however, may be intersecting burials. One mass burial contained six or more individuals randomly dispersed throughout

←

Fig. 3.—Original (1907) Hartman burial map from Las Huacas.

the pit. This pit, Burial X, was "filled with a layer of bones almost half a meter thick" (Hartman, 1907:21). No durable artifacts were interred with these individuals. Burial XV contained four individuals. The burial with "not less than fourteen metates," mentioned above, apparently was also a mass grave. At least three burials (III, V, and VI) contained two individuals; of these two were devoid of artifacts and one contained one metate. If burials I and VIII were in fact intersecting pits, it appears that one of the pits in each were double interments as well; the other intersecting pits appear to be single interments. The majority (at least eight) of the burials were single interments, six of which contained whole metates and one was devoid of artifacts.

In all cases, the skeletal remains of single interments were carefully placed in a localized portion of the pit, usually ($n = 7$) toward one edge. Double burials were likewise concentrated in one or two parts of the pit, in two cases on opposing edges of the pit (burials V and VI). Artifacts were also carefully placed within the graves in most cases. Usually the artifacts were interred among or directly over the skeletal remains, but in some cases were placed elsewhere in the grave (burials VI, XIII, XVI).

The burials at Las Huacas share some general characteristics with those from other cemetery sites excavated in southern Greater Nicoya. The Bolson cemetery, in the Tempisque River valley, is of particular importance since the site has a well-excavated suite of Zoned Bichrome period burials with well-documented skeletal and artifactual remains (Baudez, 1967:37–44, 304–305). Like Las Huacas, the primary period of cemetery usage apparently occurred during the Ciruelas phase (Baudez, 1967:44; Stone, 1977:32). The cemetery contained both single and multiple (2–3 individuals) interments in circular to oval pits, ranging in size from about 0.5–1.5 m in maximum diameter, with occasional overlap of pits. In terms of pit shape, size, and placement, the Bolson features correlate well with the Las Huacas burials; but pit depths (between about 0.3–1.2 m) generally were much shallower at Bolson. In contrast to Las Huacas, primary flexed and semi-flexed interments were encountered at Bolson, and its secondary interments were more randomly spread through the grave (although in one case three skulls were arranged at one side of the pit).

Primary flexed and extended interments were also encountered in Orso–Culebra phase burials at the Nacascolo site in the Bay of Culebra (Snarskis, 1981; Vázquez, 1986; Wallace and Accola, 1980). Although the number of individuals interred is not certain in some cases, most of the burials at Nacascolo were single interments (Vázquez, 1986). Another large Zoned Bichrome period cemetery (El Carmen) at Hacienda Mojica was also excavated, but no skeletal remains were recovered (Lange, 1984; Ryder, 1986). Day (1984) reports similar Zoned Bichrome ceramic remains from mortuary context at Hacienda Tempisque. Still other large cemetery sites, such as El Vigia (near the habitation site of Matapalo) and Las Pilas (near the Santa Elena Peninsula) are known from the region (Lange and Scheidenhelm, 1972; Sheets et al., 1991; Sweeney, 1975). Burials are also known from Nosara and Las Casitas, but the size and character of these cemeteries are not well reported (Guerrero, 1986; Ohlsson, 1991).

The use of stones to encircle or cap burial features, as reported for other contemporaneous cemeteries in Greater Nicoya (Lange and Scheidenhelm, 1972) and the adjacent highlands (Sheets et al., 1991; Skirboll, 1981), was not reported from Las Huacas. Likewise, stone "circles" or "caps" are not known from most Zoned Bichrome period cemeteries in the southern sector (Baudez, 1967; Guerrero,

Table 2.—Ceramic attributes from Hartman I subcollection.

	Vessel number								
	28	37	45	46	50	57	58	59	71
Measurements:									
Width	59.2	55.0	109.1	59.9	118.9	59.1	52.6	72.0	65.7
Height	55.0	46.3	86.4	53.8	102.6	50.1	46.1	61.2	49.9
Rim Height	6.8	11.2	18.3	13.5	19.5	12.4	10.4	10.5	6.6
Oral Diameter	22.7	22.8	48.0	19.9	58.3	20.8	17.4	25.9	18.9
Rim Thickness	3.8	4.1	3.8	5.0	7.6	4.8	4.7	4.8	3.8
Body Thickness	NA	NA	NA	NA	8.0	NA	NA	NA	NA
Weight	72.0	50.4	283.4	70.8	507.9	63.4	46.7	109.0	69.5
Manufacture/Morphology:									
Coiled	X	X	X	X	X	X	X	X	X
Temper	VG	VG	VG	VG	VG	VG	VG	VG	VG
Rim Form	st/in	in	ev	in	ev	in	in	st	in
Surface Finish:									
Average Body Color	YB	YB/GB	RB	YB	DR	YB/GB	RB	DB	RY
Slipped Body	X	?	X	?	?	?	X	X	X
Slipped Interior	X	?	X	?	?	—	X	X	?
Burnished	—	X	—	—	X	—	X	X	—
Decoration:									
Undecorated	X	—	—	X	—	—	—	X	X
Incised	—	X	—	—	—	X	X	—	—
Punctate	—	—	X	—	—	—	—	—	—
Modeled Applique	—	BE	—	—	—	BE	BE	—	—
Other	—	—	—	—	DS	—	—	—	—

Abbreviations:

- a) NA = Not available, ? = Uncertain attribution.
- b) Manufacture/morphology:
Coiled: X = vessel at least partially manufactured by coiling.
Temper: V = volcanic, G = grit.
Rim form: st = straight, in = incurvate, ex = excurvate, ev = everted.
- c) Surface finish color:
RB = reddish brown (Munsell 2.5YR 3–5/4–6) DR = dark reddish brown (Munsell 2.5YR 4–5/3–6).
RY = reddish brown–yellowish red (Munsell 5YR 4–5/3–6).
YB = strong brown–yellowish brown (Munsell 7.5YR 4–5/6, 10YR 5/4–6).
GB = greyish brown–dark greyish brown (Munsell 10YR 4–5/2–3).
DB = very dark brown (Munsell 10YR 2–3/1–2).
- d) Decoration
Other: P = painted, DS = drag stamped.

1986), although stone was used at Las Casitas near the town of Nicoya to outline the top of the burial pit (Hartman, 1907:15). Likewise, artificial stone mounds, reported from Nosarita in the lower Nosara River area (Lange, 1986) and elsewhere in southern Greater Nicoya (Norr, 1986; Ryder, 1986), were not encountered at Las Huacas, Las Casitas, or Nosara (Guerrero, 1986; Hartman, 1907). At Bolson, Nacascolo, and Hacienda Mojica, decorated metates, mace-heads, and jade were much less frequent than at Las Huacas. At these cemeteries ceramics were more common, however. Also in contrast to these other cemeteries, the Las Huacas ceramic sample has a notable predominance of small to diminutive vessels. The numerous “miniature” olla vessels in the Hartman collection, are similar

Table 3.—Continued.

Vessel number												
219	220	221	222	223	224	225	227	228	229	230	231	232
58.4	54.1	50.8	49.2	52.8	60.9	52.5	40.9	51.9	51.2	54.2	47.8	50.7
49.4	40.7	41.4	37.4	45.1	44.5	45.0	29.3	38.2	44.2	34.5	39.2	38.0
6.4	5.1	5.9	5.1	6.7	5.6	7.3	5.0	5.6	7.9	4.9	5.8	4.8
19.1	19.2	NA	19.5	21.3	23.1	18.7	17.2	16.6	18.8	16.8	15.6	14.5
4.5	3.7	3.8	3.7	4.0	5.1	4.6	4.0	3.8	3.4	3.5	3.5	4.2
NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
55.1	48.5	35.4	33.6	41.8	67.5	71.3	23.8	49.1	48.6	37.3	41.6	37.5
X VG in	X VG in	X G(V?) in	X G(V?) in	X G(V?) st/in	X G(V?) in	X VG st	X VG in	X VG st/in	X VG in	X VG st	X G(V?) in	X VG in
Ry X X —	Ry X ? —	Ry X ? —	Rb X — —	Gb ? ? —	Db X X —	Db X X —	Ry X ? —	Yb X X —	Dr X X X	Yb ? — —	Gb X X —	Rb X — —
X — — — —	X — — — —	X — — — —	X — — — —	X — — — —	X — — — —	X X — — —	X X — X —	X — X — —	X — — — —	X — — — —	X — — — —	X — — — —

Table 3.—Continued.

[illegible]

Table 3.—Continued.

	Vessel number									
	261	262	263	264	265	266	267	268	270	271
Measurements:										
Width	68.5	79.5	63.1	110.9	66.0	70.2	52.6	46.9	63.8	53.7
Height	57.1	66.5	NA	NA	NA	55.3	49.1	35.0	39.5	45.0
Rim Height	12.5	11.5	NA	NA	NA	14.3	11.5	7.3	6.0	10.0
Oral Diameter	57.5	60.5	NA	NA	NA	14.0	16.1	14.9	19.2	19.0
Rim Thickness	6.9	4.9	NA	NA	NA	4.9	4.4	4.2	4.4	4.2
Body Thickness	NA	NA	4.4	6.4	NA	NA	NA	NA	NA	NA
Weight	115.8	170.8	106.3	56.0	308.7	87.3	59.5	37.1	66.1	54.5
Manufacture/Morphology:										
Coiled	X	X	X	X	X	X	X	X	X	X
Temper	VG	G(V?)	VG	VG	VG	G(V?)	VG	VG	G(V?)	G(V?)
Rim Form	ex	ex	NA	NA	NA	in	in	in	in	in
Surface Finish:										
Average Body Color	RB	RB	RB	DG	RY	GB	GB	GB	DB	DB
Slipped Body	X	X	X	X	—	?	?	?	?	?
Slipped Interior	X	X	NA	NA	NA	—	—	—	—	—
Burnished	?	X	?	—	—	—	—	—	—	—
Decoration:										
Undecorated	X	—	?	?	—	—	—	—	—	—
Incised	—	—	—	—	—	X	X	X	X	X
Punctate	—	X	—	—	—	—	—	—	—	—
Modeled Applique	—	—	—	—	—	BE	BE	BE	BE	BE
Other	—	—	—	—	—	—	—	—	—	—

to those found in other funerary assemblages in southern Nicoya related to the period A.D. 100–500 or later.

In some cases, large cemeteries are located in the vicinity of village sites (Baudez, 1967; Lange and Scheidenhelm, 1972; Sheets et al., 1991; Sweeney, 1975). The location of a Zoned Bichrome village that would relate to the Las Huacas burial ground remains undetected, however. In several instances, there is evidence that some members of the community were buried within the village (Lange, 1984), as was the case at Vidor (Orso–Mata de Uva phase) and Matapalo (Monte Fresco phase) where infants were buried in inverted urns within the village site (Coe and Baudez, 1961; Lange, 1980). Possible urn burials have also been reported for the Rivas Isthmus area (Healy, 1980:49).

Throughout southern Greater Nicoya there is considerable variability in mortuary practices during the Zoned Bichrome period in terms of the treatment of skeletal remains (primary or secondary), the number of individuals in discrete graves, and particularly the variability in grave offerings within and between cemeteries. This variability has often been interpreted as indications of differential status within the social group (e.g., Lange, 1984; Snarskis, 1981; Stone, 1977); however, as is discussed below, caution must be exercised in assigning social meaning to these often poorly known burial grounds.

MATERIAL REMAINS

A total of 485 objects were recovered during Hartman’s investigations at Las Huacas; 80 of these artifacts were actually excavated and recorded by Hartman.

A wide variety of lithic and ceramic artifacts are present in the combined Hartman collections. Two cuttlefish shell beads recovered from disturbed Burial XVII are the only artifacts not manufactured from stone or ceramic in the combined Hartman collections, although metal artifacts are present in the Velasco I collection from the site (Hartman, 1907:27). Lithic objects included: plain and decorated metates (HI = 15, HII = 15), club/mace heads (HI = 2), amulets/pendants (HI = 19, HII = 40), celts (HI = 5, HII = 95), beads (HI = 12, HII = 20), "barkscrapers" (HI = 1, HII = 2), polishing stones (HI = 7, HII = 28), and obsidian fragments (HII = 2) (for further discussion of lithic remains see Fonseca and Richardson, 1978; Fonseca and Scaglion, 1978; Hartman, 1907).

Ceramic objects from the Hartman I subcollection, including small globular vessels ($n = 9$), figurines ($n = 3$), and ocarinas/whistles ($n = 2$), are the primary focus of the following discussion. Of the 200 ceramic objects from the Hartman II subcollection, which also includes small globular vessels ($n = 59$), figurines ($n = 16$), and ocarinas ($n = 10$) as well as other ceramic forms, only the small globular vessels are discussed here due to the uniformity of these vessels and their conformity with those excavated by Hartman. As a group these vessels are by far the most common ceramic form in both Hartman subcollections.

Small globular vessels.—The total of 68 small globular vessels (HI = 9, HII = 59), summarized in Tables 2 and 3, are separated into two primary categories (described below) based on overall morphology and decoration. All these small vessels (*ollas*) share several basic similarities with regard to manufacture and composition. All vessels were manufactured by coiling, although it is not certain that coiling was the only technique employed and some may have been manufactured by adding coils to a molded base. Since the majority of vessels are whole, however, detailed information regarding manufacture or the internal composition of the pots is limited in most cases to surface attributes.

The small globular vessels were manufactured with a fine- to medium-bodied paste, well consolidated in all cases. Extrusive temper, observable on exterior surfaces and on fracture surfaces of the few broken vessels, is grit in all vessels. There is some question about non-plastic inclusions in Costa Rican pottery as to whether they occurred naturally in the clay sources or were culturally added as temper (Sweeney, 1975). The non-plastic inclusions in the small vessels seem to be a true temper, although petrographic analysis is needed to confirm this assessment. The presence of inclusions of volcanic origin in the ceramic paste is a region-wide characteristic of Zoned Bichrome ceramics and, based on compositional analysis from Greater Nicoya ceramics, it is likely that potting clays typically were obtained locally (Bishop et al., 1988).

When temper composition was clearly visible, temper included a variety of minerals, apparently from weathered igneous rocks of volcanic origin, and notably, volcanic tuff. Considerable variation was observed in the size of the mineral and volcanic tuff constituents and in the percentage of temper in various vessels (typically ranging between 30–50%). This may be indicative of several source locations or variable processing of temper stone or clay.

The small globular vessels were separated into two primary categories based on several distinguishing features which included body and especially rim form, slip, vessel size, and decoration. The first general form consists of small *olla* vessels with strongly excurvate to everted rims; decoration (when present) occurred as rings of punctations or drag-stamped design on the shoulder of the vessel. These

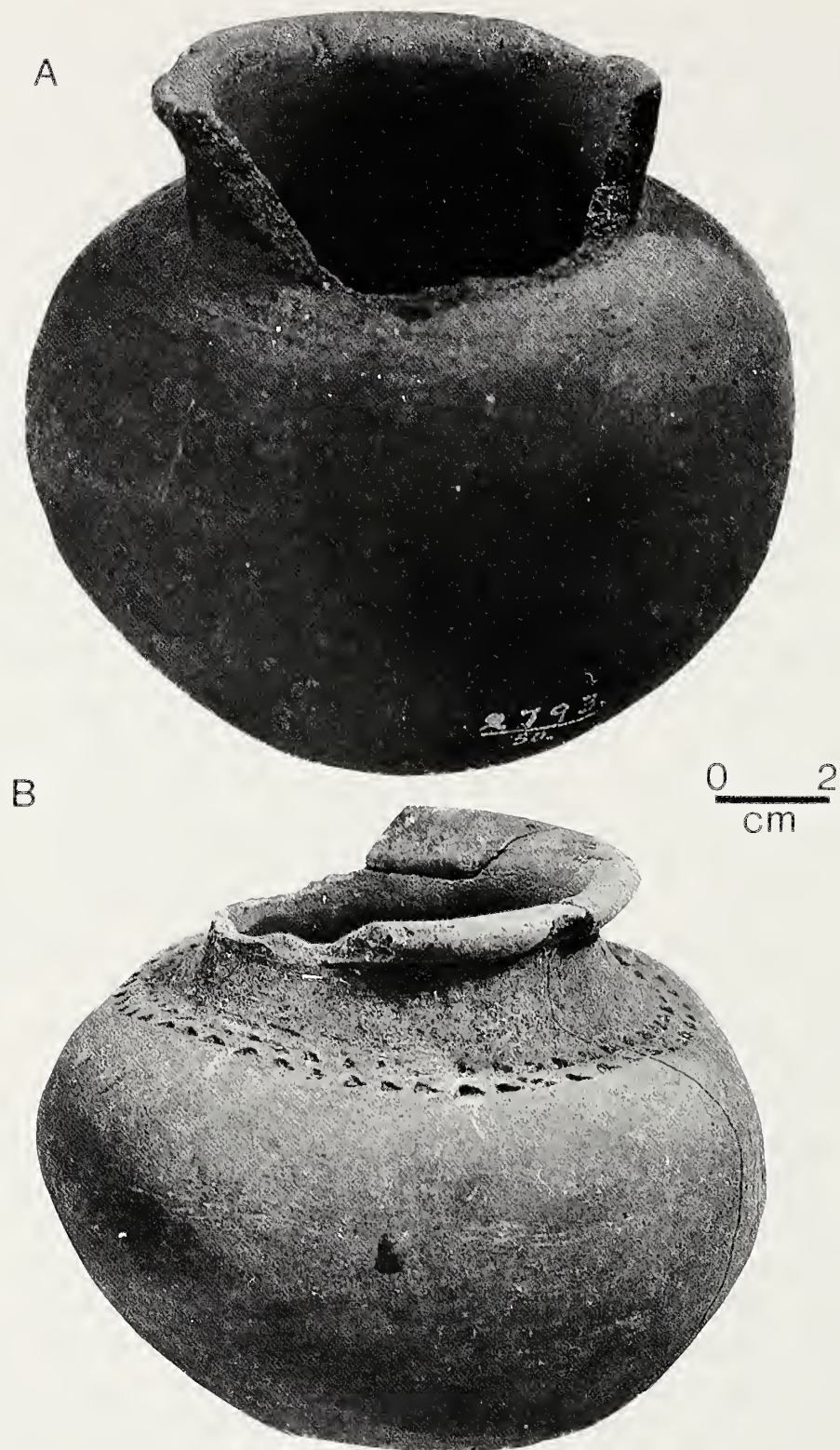


Fig. 4.—Excurvate/everted rim vessels from Hartman I subcollection. A, (2793/50) Mojica Impressed, Mojica variety; B, (2793/45) Cervantes decorative mode (Mojica Impressed, Laguna variety).

vessels had a reddish slip or in two cases were unslipped. The ten vessels attributed to this form can be further separated into three variants.

The first variant is represented by at least one vessel (HI: 2793/50) (Fig. 4A). Another vessel (HII: 2793/265) is also likely attributable to this form, but its entire upper half is broken off and therefore its rim form and decoration are not apparent. This broken vessel is virtually identical to vessel 50 in lower body shape and color. Vessel 265, being broken, is one of the few in which temper can be directly observed and measured. In vessel 265, volcanic tuff comprises over 50% of the temper with often large chunks of tuff (maximum size = 2.0–2.5 mm). Vessels 50 and 265 are globular in body form and unslipped. Vessel 50 has an

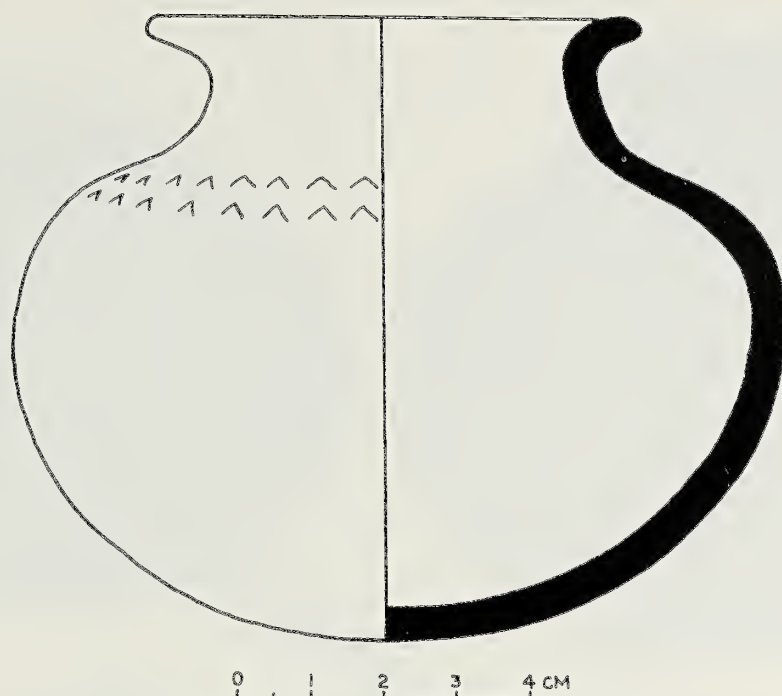


Fig. 5.—Profile of vessel 2793/45.

everted rim form and is decorated with one ring of stamped decoration, made by drag stamping with a dentate tool or seashell, identical to the Mojica Impressed variety (Baudez, 1967:325; Hoopes, 1984:133).

The second variant, represented by one vessel (HI: 2793/45), is generally globular, but has a somewhat squarish outline in planview (Fig. 4B, 5). The vessel has a strongly everted (flared) rim and two concentric rings of wedge-shaped punctations ringing the vessel shoulder, similar to the Cervantes Punctate decorative mode (Baudez, 1967:356; Lange et al., 1976) or Mojica Impressed, Laguna variety (Hoopes, 1984:133). A reddish-brown slip applied to vessel 45 is clearly apparent only on the upper half of the body and both exterior and interior surfaces of the rim.

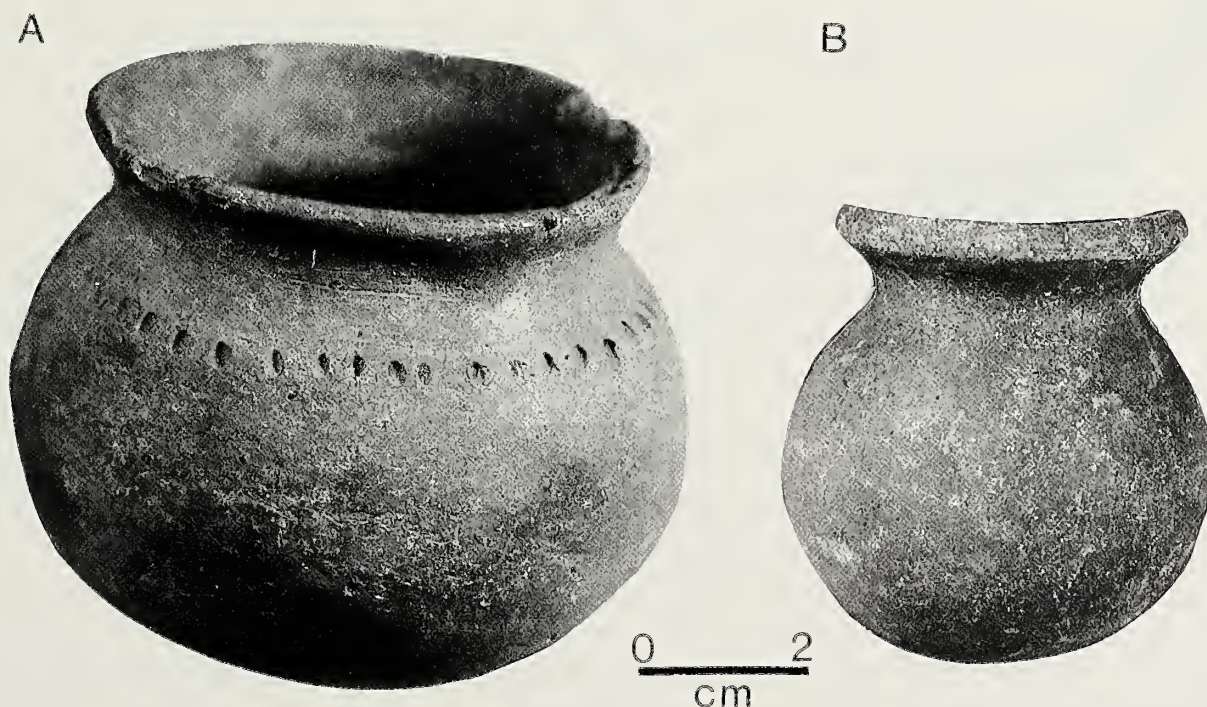


Fig. 6.—Excurvate rim vessels from Hartman II subcollection. A, Congo Punctate, 2793/262; B, 2793/257.

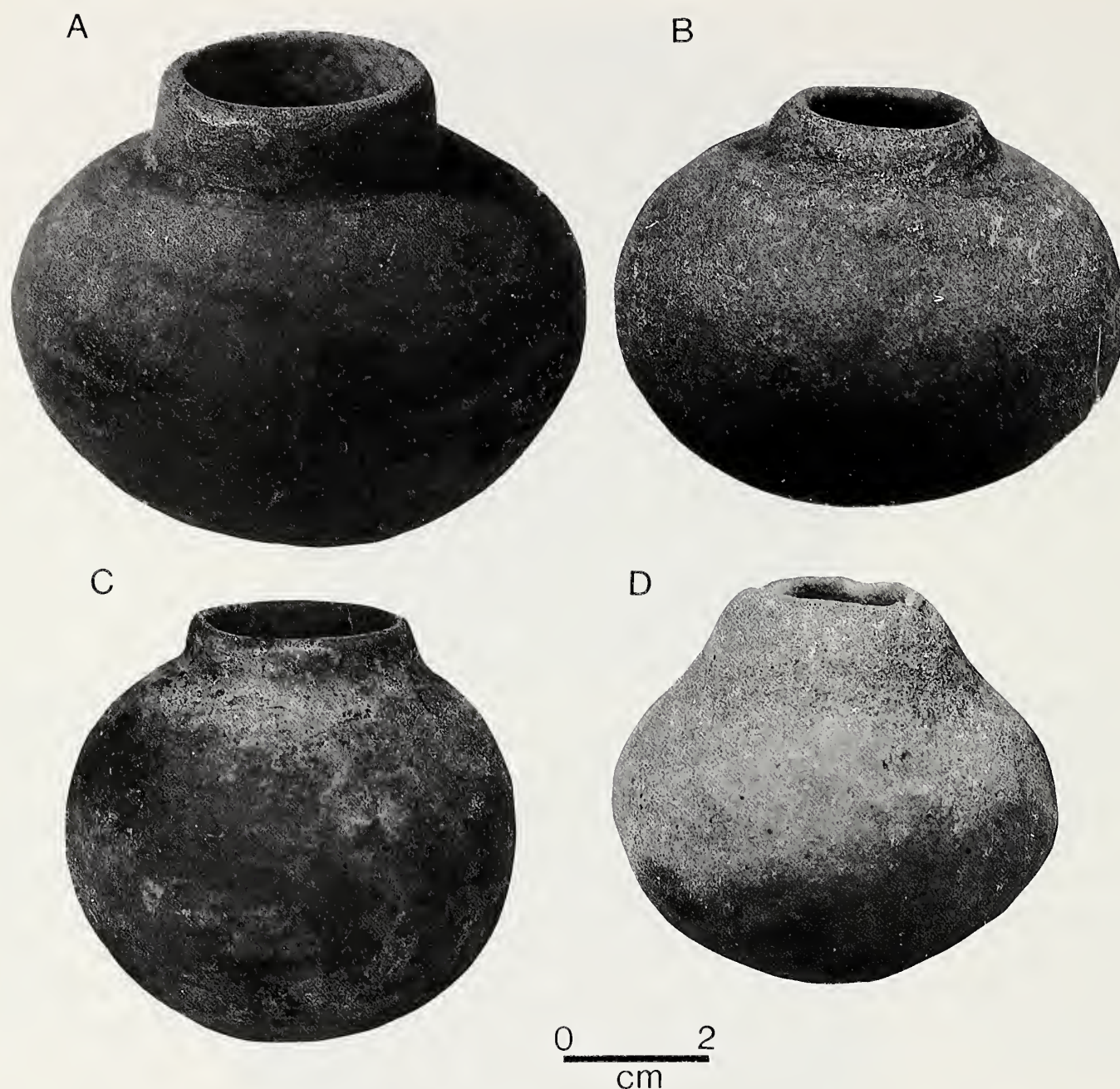


Fig. 7.—Miniature globular vessels (Guinea Incised/Urruela Red) from the Hartman I subcollection. A, 2793/59; B, 2793/71; C, 2793/28; D, 2793/46.

The third variant is represented by five vessels (HII: 2793/256, 258–262). These forms have excurvate rims attached to low- to medium-height bodies. In general, these vessels have a large oral diameter in relation to overall vessel size. A reddish colored slip was applied to all exterior surfaces and rim interior. In one case, there is a circular ring of punctations used for decoration on the shoulder of the vessel (Fig. 6A). This form is similar to the Congo Punctate variety attributed to the Ciruelas phase at the Bolson cemetery (Baudez, 1967:329). Two vessels (2793/256–257) are also similar in shape to the other five vessels; however, they differ in body and oral diameter dimensions and color (Fig. 6B).

The second primary form of small to diminutive globular vessels ($n = 52$) is represented by two variants. The first, virtually identical to the Urruela Red form shown by Baudez (1967:349), is characterized by incurvate to straight rims formed by the attachment of an additional coil to the body (Fig. 7A–C, 8). In most cases, there is a pronounced angle between the body and the rim. These forms typically

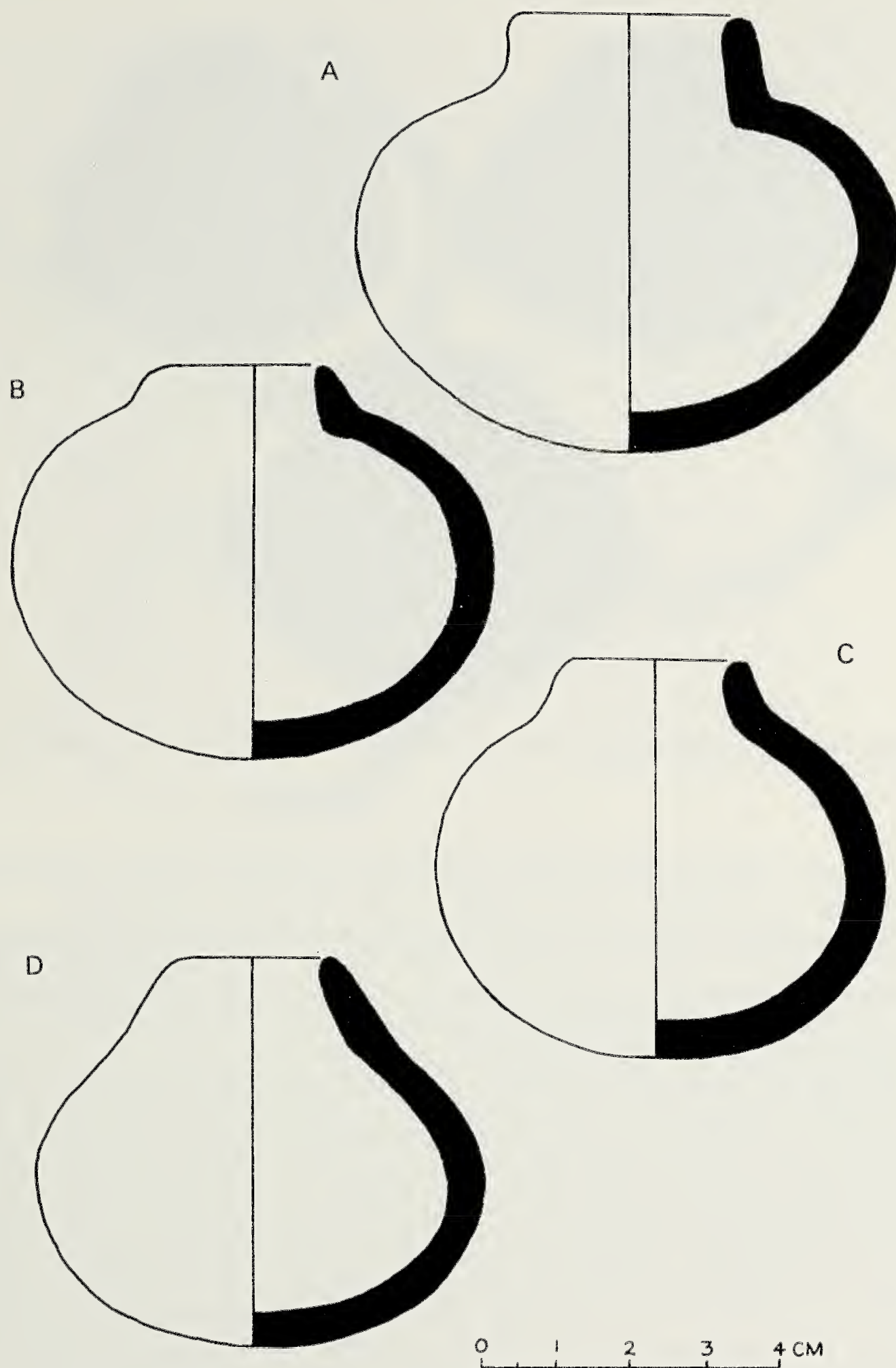


Fig. 8.—Profiles of vessels in Fig. 7.



Fig. 9.—Miniature bird-effigy vessels (Guinea Incised, Guinea variety) from Hartman I subcollection. A, 2793/57; B, 2793/58; C, 2793/37.

have reddish-brown to blackish slip and exhibit a smoothed, almost polished in some cases, or burnished exterior surface. These vessels are undecorated.

These vessels are attributed to the Ciruelas phase at the Bolson cemetery, where, as at Las Huacas, they were associated with Guinea Incised ceramics (Baudez, 1967:41). Small *olla* forms, virtually identical to varieties from Las Huacas, have also been recovered from the Early to Middle Polychrome period cemetery of Los Angeles on Ometepe Island (Haberland, 1992:95).

The second variant differs slightly with respect to rim and body form, color, and surface treatment (Fig. 7D). These vessels have incurvate rims which are basically an extension of the vessel body with a less pronounced angle at the juncture of the rim and body (Fig. 8, bottom profile). These forms are generally slipped with tan or yellowish brown slip, although in some cases slipping is not certain, and are smoothed but not polished or burnished. They are sometimes decorated with pellet and strip applique used to create a bird-like appearance with incision over the wings, beaks, or tails in some cases (Fig. 9, 10). The bird effigy vessels are uniform in form and decoration with two exceptions. One vessel (Fig. 11A) is similar in body form but with more embellished incising and punctuation. The second vessel (Fig. 11B) has a pronounced neck with a strap-handle positioned opposite the bird-effigy face. The bird-effigy vessels are all attributed to the Guinea Incised, Guinea variety (Bonilla et al., 1987). Within the entire sample of small vessels, no definitive distinction can be made between the two variants of this

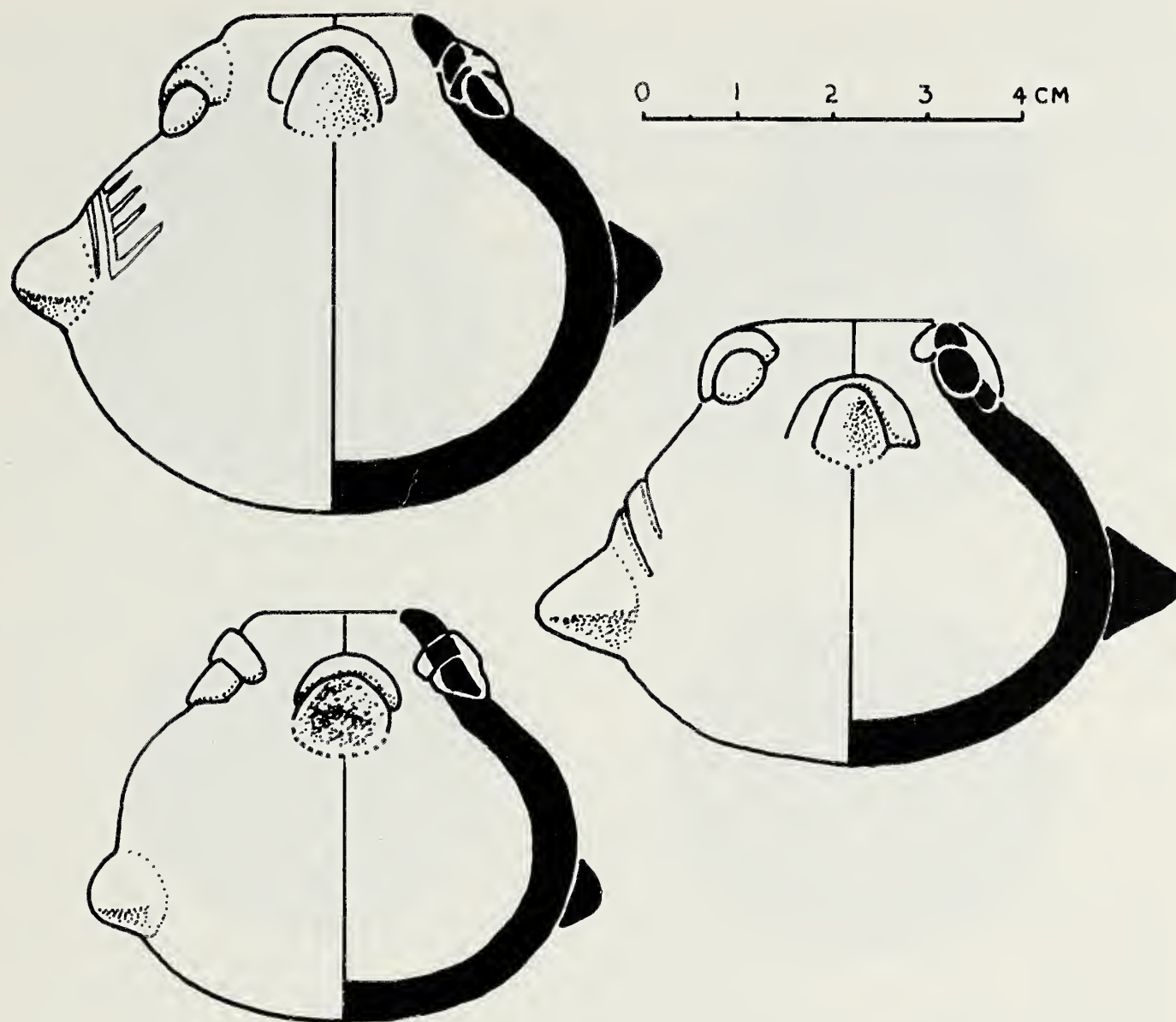


Fig. 10.—Profiles of vessels in Fig. 9. A, top; B, bottom; C, right.

form on the basis of body and rim form or surface treatment, and the two inter-grade quite subtly.

Several additional small vessels, which do not correspond with any of the forms summarized above, are included in the analysis and merit mention. The only painted “miniature” vessel (Fig. 11C) is likely related to the Charco Black on Red type. Another “miniature” vessel with a modeled coil attached to the shoulder has affinities to the Cervantes decorative mode (Fig. 11D; Baudez, 1967:356). A small black vessel with two strap handles attached to the rim and shoulder of the vessel was ritually killed prior to interment (Fig. 11E, F). This vessel has an incised chevron design on the neck reminiscent of Ballena Incised ceramics associated with the Catalina phase in the Tempisque River Valley (Baudez, 1967:335). One other vessel (2793/263) is a small carinated vessel with a bright red slip. This vessel is similar to forms from the highlands associated with the Curridabat sandy applique *olla* form (cf. Skirboll, 1984b:66, fig. 13).

Ceramic figurines.—Three effigy figurines were recovered from burials excavated by Hartman. The first (2793/3), from Burial I, is an anthropomorphic (female) figurine (maximum height = 104 mm; weight = 194.3 g) (Fig. 12, 13). The figurine is hollow and may have been manufactured from a mold as reported elsewhere for similar figurines (Healy, 1980). There is a perforation through the

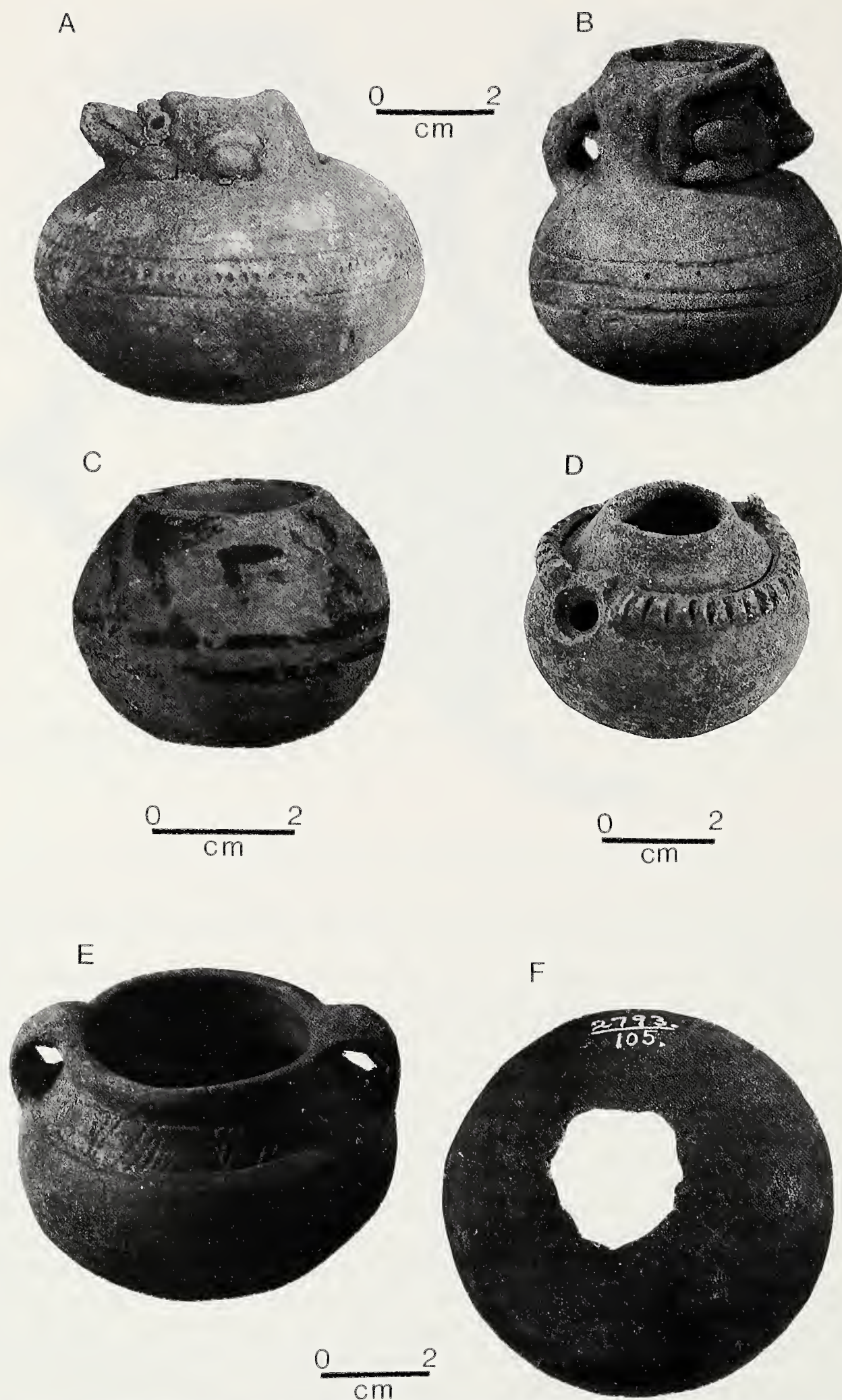


Fig. 11.—Miniature vessels from the Hartman II subcollection, including variant bird-effigy forms. A, 2793/266; B, 2793/106; C, 2793/212, painted (Charco Black-on-Red) vessel; D, 2793/107, vessel with attached coil; E, F, 2793/105, killed incised (Ballena) vessel.

neck and punctations to represent nostrils. The neck perforation may have been used to hang the figurine.

A tan slip (Munsell 5 YR 6–7/4–6) was applied to the entire exterior of the figurine. Additional pigments were used in various places to embellish the figure. The pigments included reddish-brown (Munsell 2.5 YR 4/6–8) and black (5 YR 2/2) colors.

The figurine is adorned with a headpiece and earspools, both highlighted with pigments. The face, breasts, arms and waist–groin area are likewise painted and may represent body painting, tattooing, or garments (Carlsen, 1988).

The figurine is attributable to the Galo Polychrome, *Figura* variety (Bonilla et al., 1987). Hartman (1907:16) notes that “figurines of this type are of rather common occurrence in this burial ground,” as attested by other examples in the Hartman II subcollection and the Velasco I collection. Nearly identical figurines were recovered from the Matapalo site in the Bay of Tamarindo and associated with the Matapalo phase (radiocarbon dated to A.D. 640 \pm 50 at the site) (Sweeney, 1975:35, 617:plate 84). Although Galo Polychrome is widely distributed throughout Greater Nicoya, specialized forms including female figurines apparently do not occur in the northern sector (Lange et al., 1992:84), but they are common throughout the southern sector (Bonilla et al., 1987:137; Lothrop, 1926: plate CXXIV; Snarskis, 1981:182).

Another human-like figurine (2793/19) was recovered from Burial VIII (height = 105 mm; weight = 174.4 g) (Fig. 14, 15). The figurine, with both human and simian (especially in the face) characteristics, is holding an infant and seated on a four-legged stool or metate with stylized zoomorphic (amphibian/reptilian) heads on either side. The figurine was manufactured by attaching a hollow barrel-shaped piece, comprising the body, to a solid flat slab which represents the metate/stool top. Applique coils, strips, pellets, and slabs were used to form the appendages and facial features of the figure as well as the infant and zoomorphic adornos. Incision and punctation was employed to highlight various features of the figure and the modeled headpiece.

The figurine was manufactured with fine-bodied clay paste with volcanic grit temper. No painting or slipping is apparent on the figurine. A large hole (9.8 mm in diameter) in the back of the body may have been made to prevent breakage during firing. A perforation through the head above the ears may also have been employed to facilitate firing, but, like the Galo Polychrome figurine, may have served to suspend the figurine.

The second figurine relates to the Guinea Incised, *Guinea* variety (Bonilla et al., 1987) and has correlates throughout the southern sector of Greater Nicoya (Ferrero, 1981:94; Lines, 1934:75; Lothrop, 1926:266; Snarskis, 1982:43).

A third figurine (2793/56), from Burial XVII, is a bird-effigy manufactured from a small globular vessel similar to those described above (height = 69 mm; weight = 79 g) (Fig. 16). The head, tail, and possibly legs are hollow globular pieces of clay attached to the body. The feet, eyes and nostrils were made from applique buttons attached to the body. The beak and wings are flattened strips of clay. Several holes are present behind the eyes and under and above the tail.

The body, head, tail, and legs were smoothed but no other surface treatment was apparent. The ceramic paste is fine bodied and well consolidated with grit temper. The figurine's color is tan (Munsell 2.5 YR 5/4). This figurine was originally interpreted (Hartman, 1907:27) as a whistle, but it likely was not used as such. Based on its association and similarity to Guinea Incised bird-effigy vessels,



Fig. 12.—Galo Polychrome, Figura variety figurine (2793/3) from Burial I. Darker color is dark brown to black pigment; headpiece, "girdle," and earspools are reddish-brown pigment.

the figurine can be attributed to the Guinea Incised, Guinea variety (Bonilla et al., 1987).

Ceramic pestle.—One oblong pestle, recovered from Burial VIII, was manufactured using a solid block of fine- to medium-bodied well-consolidated clay

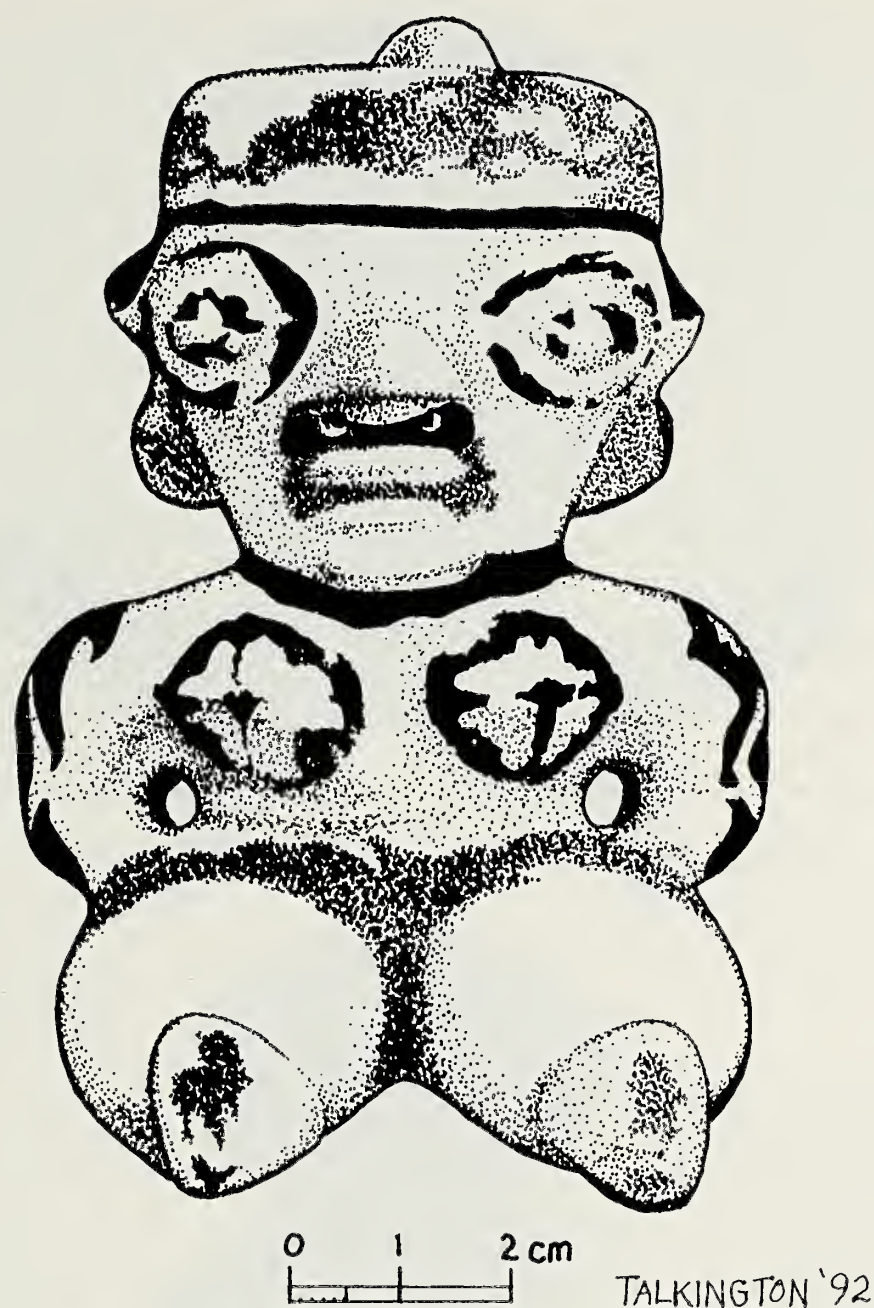


Fig. 13.—Drawing of Galo Polychrome figurine.

with grit temper (Fig. 17A). An applique adorno is attached to the top of the pestle and represents a human-like or simian face. The bottom of the pestle did not exhibit use wear, but the edges of the base did show evidence of abrasion. The pestle was burnished on the sides, no slip was applied. There is a perforation near the top of the pestle running perpendicular to the adorno face. The pestle is 115.6 mm in length, 4.8 mm wide at the base, and weighed 182.3 g. The figurine is directly associated with the Guinea Incised human-like figurine (2793/19).

Ceramic ocarinas.—Two ceramic ocarinas or whistles were recovered from burials IX and XVII. The ocarina from disturbed Burial XVII represents an armadillo (length = 56 mm; weight = 35 g) (Fig. 17B). The hollow ovoid body is covered by a ceramic slab meant to represent the armadillo's shell. The body is embellished with four molded legs and two ears. The "shell" is decorated with four incised lines and punctations. The exact method of manufacture is unknown, but the ocarina appears not to be mold-made. No evidence of slipping or burnishing is apparent. The overall color is reddish-brown (Munsell 5YR 5/4).

The ocarina from Burial IX is an ovoid-bodied hollow whistle with a distinct

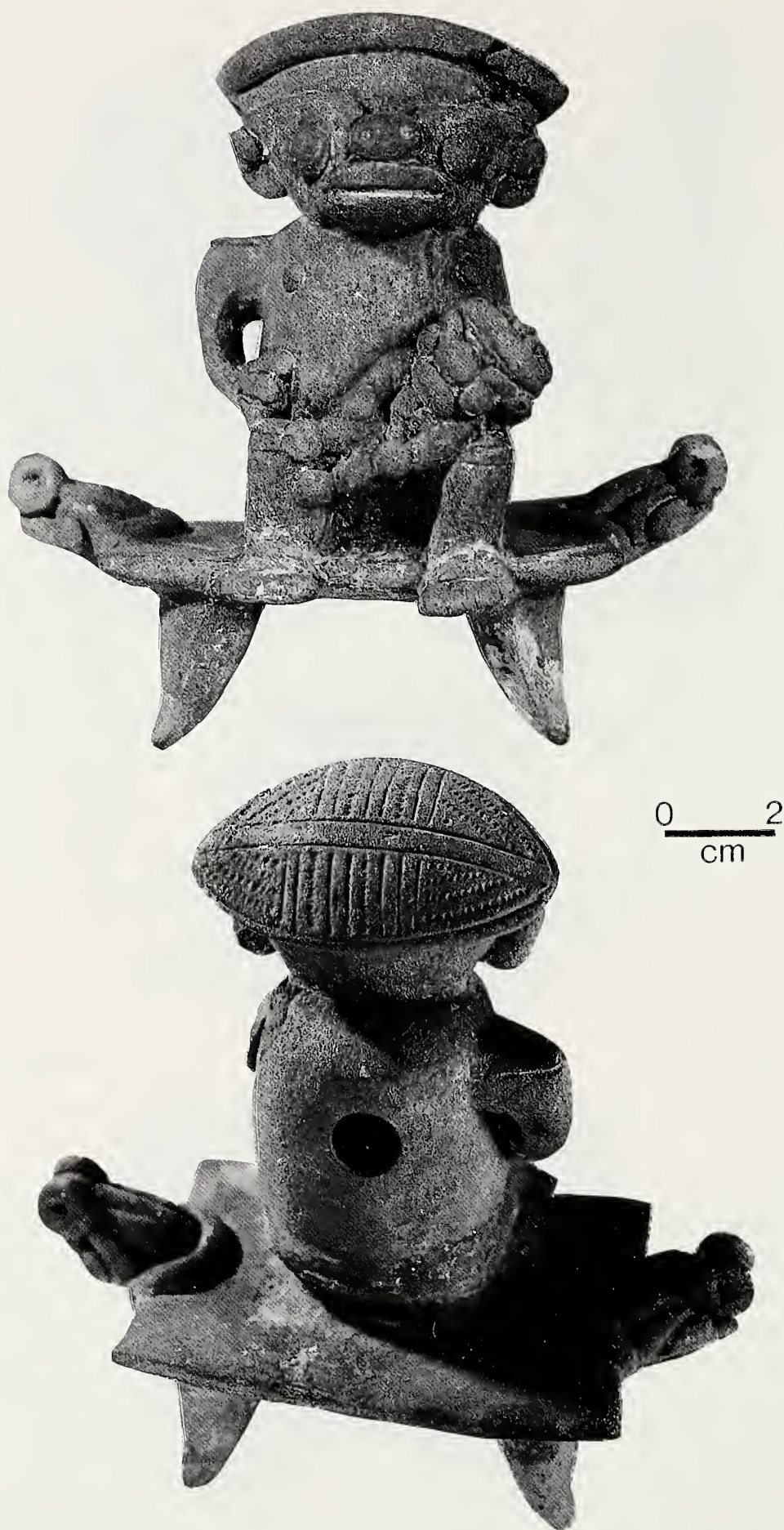
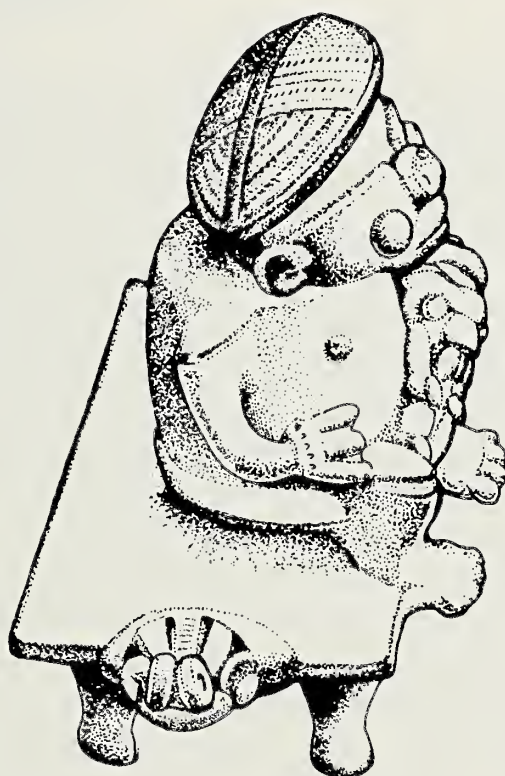


Fig. 14.—Guinea Incised figurine (2793/19) from Burial VIII.

mouthpiece and finger hole opposite an appliqued “bat-like” adorno face at the base of the mouthpiece (length = 90 mm; weight = 75 g) (Fig. 18, 19). Incised lines and zoned punctation decorate the front and sides of the body. Four holes are placed within the area of zoned punctation. The method of manufacture is



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Fig. 15.—Drawing of Guinea Incised figurine.

unknown. The ocarina surface is polished and a black slip (10YR 2-3/1) was applied to the entire surface.

Both ocarinas are clearly associated with the Marbella Incised and Punctate form which is largely restricted to southern Greater Nicoya and has been widely recovered from both funerary and domestic contexts in the Bay of Tamarindo

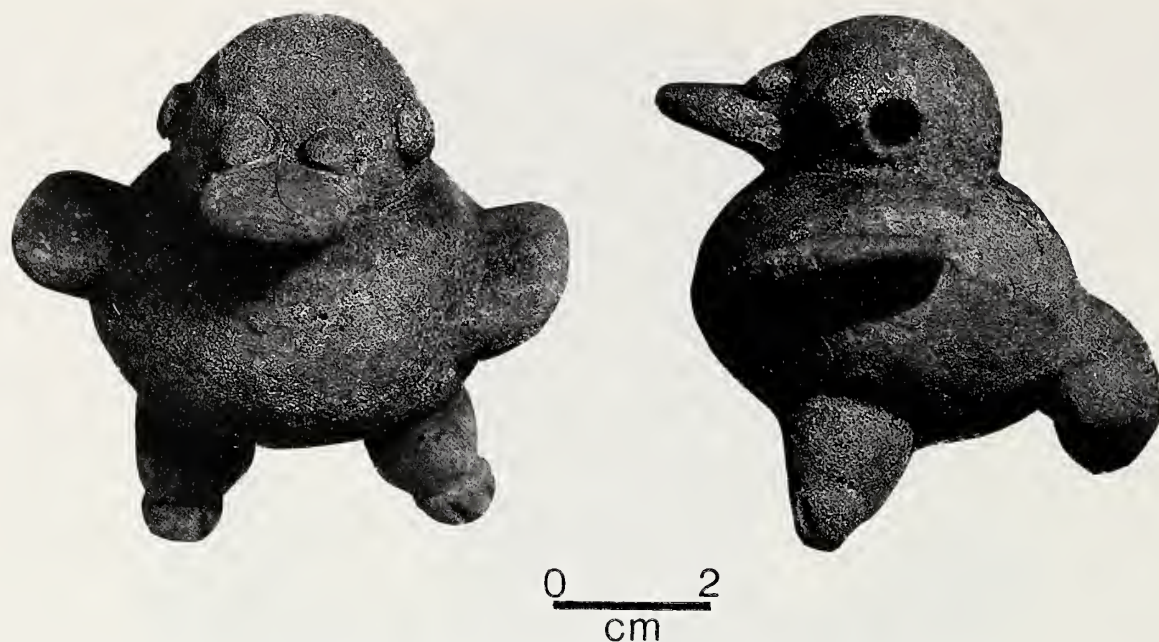


Fig. 16.—Bird-effigy figurine from disturbed Burial XVII.

(Sweeney, 1975:429), the Nosara valley (Guerrero, 1986), the Tempisque valley (Baudez, 1967:102–105; plate 25D–26A–B; Day, 1984) and elsewhere (Bonilla et al., 1987:105; Snarskis, 1982:28; Ferrero, 1981:lamina II). A unique “doughnut-shaped” ocarina (HII; Fig. 20) also shares affinities with the Marbella Zoned Impressed Punctate type.

DISCUSSION

The Las Huacas cemetery is largely attributable to the Zoned Bichrome period of Greater Nicoya (Lange, 1984); its exact affiliation with local complexes of the period, however, is less well known. This study aims to describe more thoroughly the ceramics from well-recorded burial contexts at Las Huacas to help place them within the regional typological and chronological framework established since the publication of Hartman’s 1907 report on his investigations in northwest Costa Rica. The ceramic analysis combined with examination of burial contexts at the site allows a more refined interpretation of the site in a regional context.

Fonseca and Scaglione (1978:282–284) attribute the Las Huacas cemetery to a timespan of ca. A.D. 180–525, based on the apparent preponderance of Ciruelas phase ceramics, which are somewhat more tightly dated to ca. A.D. 300–500 (Late Period IV), and those ambiguously attributable to either the Ciruelas phase or the preceding Catalina phase. The absence of radiocarbon dates at Las Huacas precludes a more precise temporal placement for this cemetery. Use of the site during the Catalina phase is indicated by the presence of certain ceramic types in the Hartman II subcollection, most notably Bocana Incised Bichrome, Bocana, and Diria varieties (Hartman, 1907:plate II). Other possible Catalina phase ceramic types, including Rosales Zoned Incised, Ballena Incised, Charco Black on Red, Marbella Zoned Impressed Punctate, Congo Punctate, and Mojica Impressed, are also represented in the Hartman II subcollection; however, these types may be transitional to or related to the Ciruelas phase (Bonilla et al., 1987).

As has been established elsewhere in the Greater Nicoya region, the distribution of Las Huacas ceramics in excavated burials indicates that the ceramic types associated with various Zoned Bichrome phases overlap considerably (Baudez, 1967; Healy, 1980; Lange et al., 1984). In fact, an examination of available

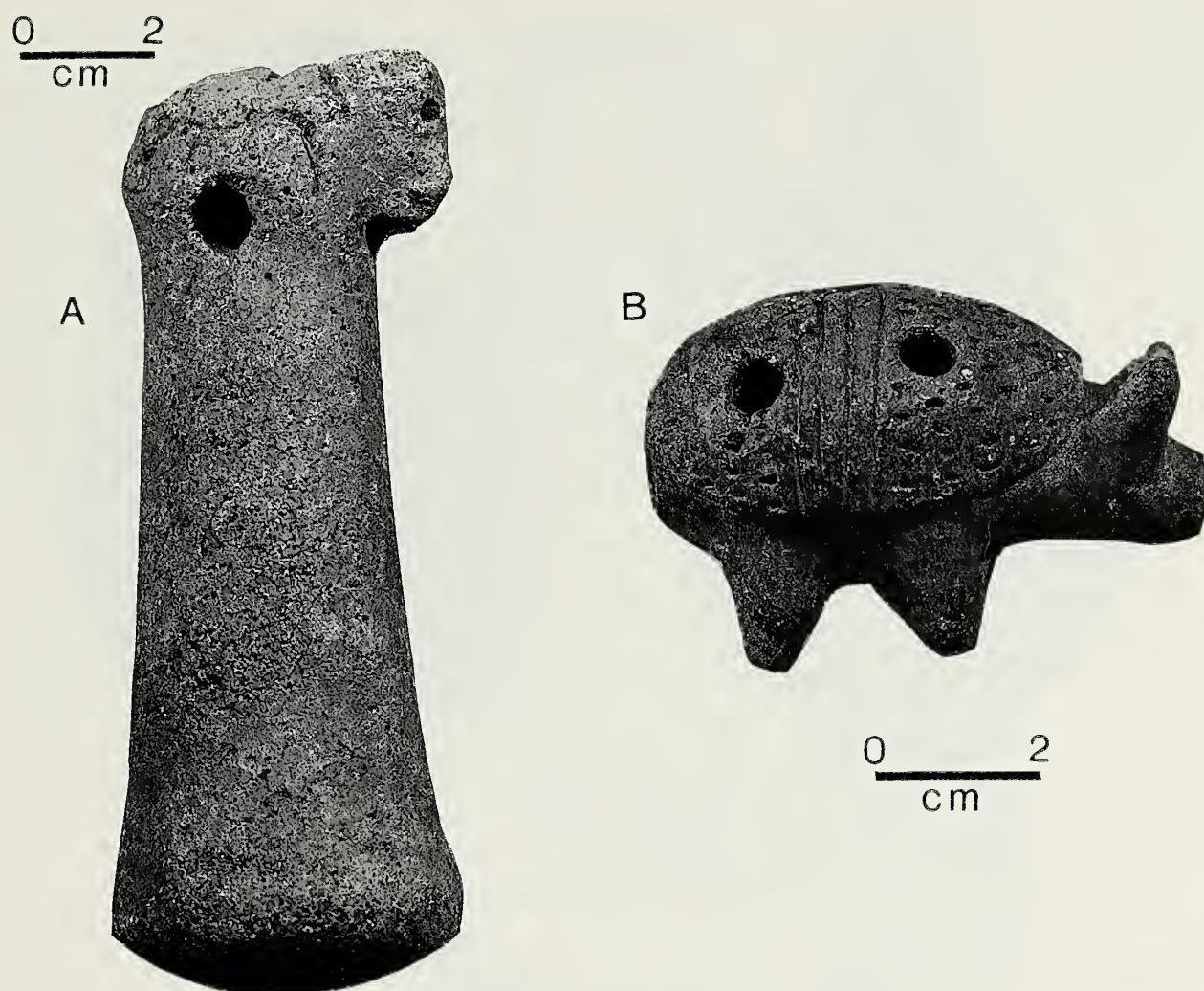


Fig. 17.—A, ceramic pestle (2793/18) from Burial VIII; B, ceramic armadillo Marbella ocarina (2793/55) from disturbed Burial XVII.

radiocarbon dates for the two phases and the distribution of related ceramics in individual cemeteries or even single burial lots demonstrates that the two phases are arbitrarily divided (Baudez, 1967; Bonilla et al., 1987; Healy, 1980; Lange et al., 1992). In disturbed Burial XVII at Las Huacas, for example, Guinea Incised/Guinea variety bird-effigy pots, Guinea Incised/Urruela Red miniature vessels, a Mojica Shell Impressed (2793/50) vessel, a Marbella ocarina, and possibly the Cervantes vessel were associated in a cluster near the center of the burial (*see* Fig. 3). Thus, it is not possible to attribute most individual ceramic forms at Las Huacas to either the Catalina or Ciruelas phase exclusively, and site usage may well predate the date of A.D. 180 suggested by Fonseca and Scaglione (1978).

Hartman recovered one Galo Polychrome figurine (San Bosco phase) from Burial I, which supports Fonseca and Scaglione's (1978) assertion that cemetery usage continued into the Early Polychrome period. San Bosco phase ceramics (Galo and Carrillo Polychrome) are common in the Hartman II and Velasco I subcollections, although they are far outnumbered by Zoned Bichrome types. The co-occurrence of Ciruelas and San Bosco phase ceramics in single burials has been reported at the Bolson and El Carmen (Hacienda Mojica) cemeteries (Baudez, 1967; Ryder, 1986). Although there are no direct associations in the Las Huacas burials, the contemporaneous use of San Bosco polychrome types with ceramic types of the Zoned Bichrome period at the site is also probable. A terminal date cannot be suggested for the Las Huacas cemetery but, given the predominance of

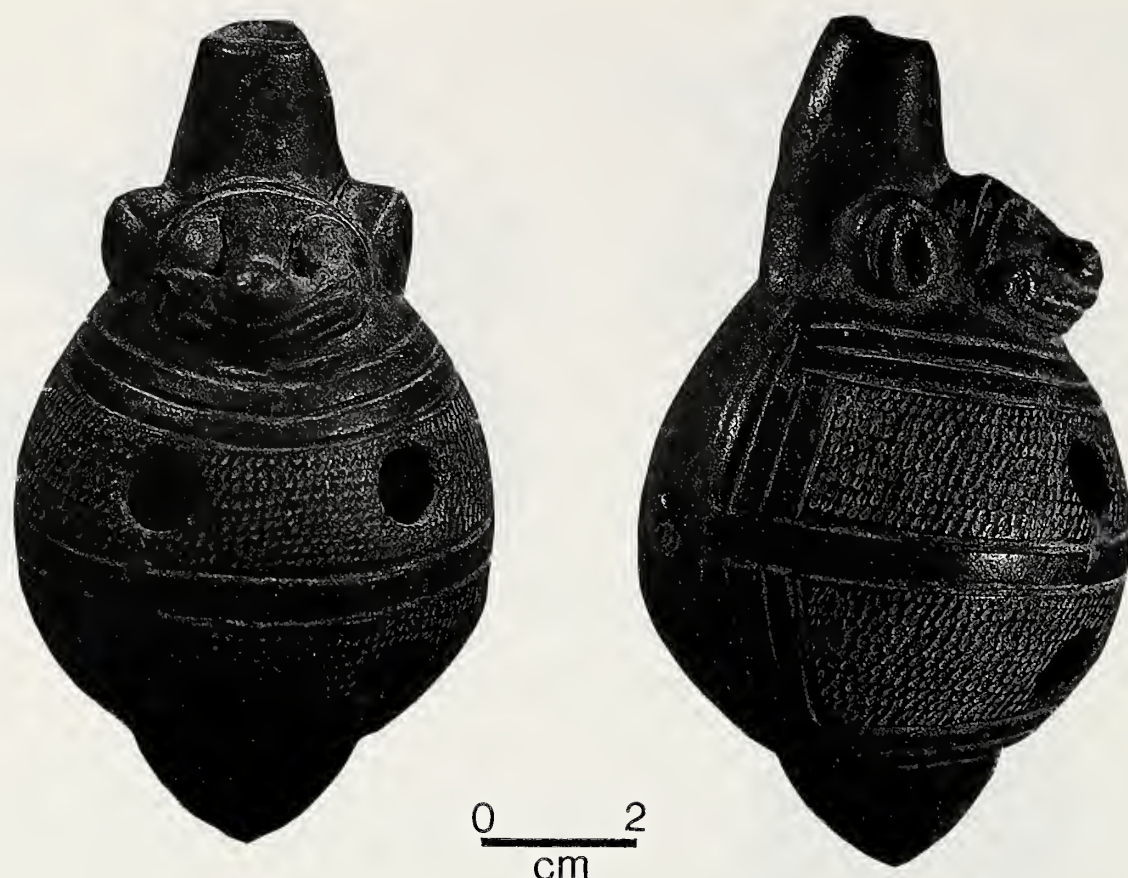


Fig. 18.—“Bat-face” Marbella ocarina (2793/21) from Burial IX.

Zoned Bichrome ceramics, it seems likely that site usage declined roughly coincident with the inception of the Early Polychrome period, ca. A.D. 500, as suggested by Fonseca and Scaglion (1978:284). The few Middle and Late Polychrome period pieces in the Hartman II and Velasco I subcollections are likely not related to the burials from the site (Fonseca and Scaglion, 1978:283).

The ceramic remains from Las Huacas correspond well with the ceramic sequences from elsewhere in southern Greater Nicoya. As with other southern sector sites, Las Huacas shows general affinities with the ceramic complexes of Pacific Nicaragua (Healy, 1980; Lange et al., 1992) and those from the periphery of Greater Nicoya in the highlands (Hoopes, 1984; Norr, 1986; Sheets et al., 1991). Pan-regional ceramic types, such as Bocana (Bocana and Diria varieties), Mojica, Rosales, and Charco Black-on-Red (Bonilla et al., 1987), are well represented in Las Huacas collections. These types are generally outnumbered, however, by ceramic types (e.g., Guinea Incised and Marbella Zoned Impressed Punctate) considered typical of southern sector sites. The abundance of jadeite or greenstone artifacts and scarcity of obsidian (two fragments) at Las Huacas also corresponds well with southern sector sites (cf. Bishop et al., 1988).

Another aspect of the site which bears on regional patterns is the high frequency of lithic artifacts (metates, pendants, beads, celts, and mace-heads) in proportion to ceramics. Lange (1986:168) points out that cemeteries with numerous greenstone artifacts and metates have limited quantities of ceramics, and vice versa. The abundant-lithics pattern is evident at the Las Huacas and Nosara cemeteries, while the more northerly Bolson, El Carmen (Hacienda Mojica), and Nacascolo cemeteries have mostly ceramics (Fig. 1). This distribution seems to imply a geographic division corresponding to the central Nicoya Peninsula, but quantities

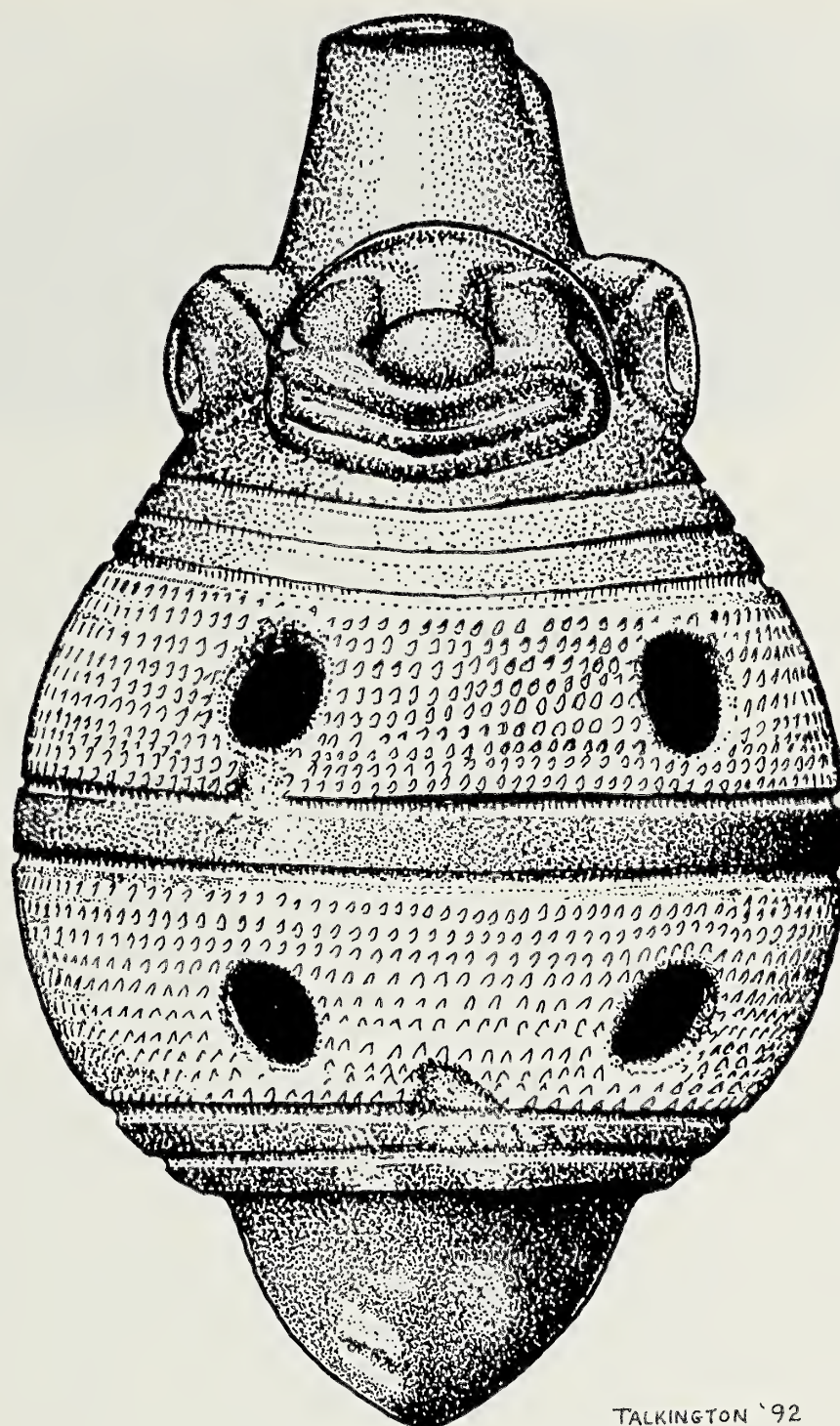


Fig. 19.—Drawing of “bat-face” ocarina.

of metates were also recovered from the disturbed Las Pilas cemetery in extreme northwestern Costa Rica (Lange and Scheidenhelm, 1972).

With regard to the metates themselves, there has been some debate regarding their function prior to interment; that is whether they, in fact, served as grinding stones or instead were used as ceremonial stools or “seats of power” (cf. Lange, 1984; Snarskis, 1984). This debate has obvious implications for their significance as offerings in the burial ritual. At Las Huacas, it seems certain that at least some



Fig. 20.—Doughnut-shaped ocarina (2793/111) from the Hartman II subcollection.

metates, primarily those that are undecorated, were used prior to their interment as grinding stones based on the use-wear evident on their grinding surfaces. Decorated examples (generally with longer legs) usually exhibit little or no use-wear. However, because an object was not used prior to its interment does not preclude the possibility that its intended function was as a grinding stone.

Regardless of function, metates and other lithic artifacts, notably pendants/amulets and mace-heads, have frequently been interpreted as “prestige goods” reserved for high ranking individuals (Tillet, 1988). Based on available regional data, it seems premature to argue that these artifacts are direct reflections of status differences. The data from Las Huacas, in fact, seem to contradict what would be expected in a burial ground where marked differences in status (i.e., chiefs or elites versus commoners) were overtly reflected in burial practices. Instead, “prestige goods” are widely distributed. Over half of the excavated burials at Las Huacas contained metates; of these, only one also contained a mace-head and three also contained pendants. Furthermore, Velasco apparently recovered more than 2000 metates at the Las Huacas burial ground (Hartman, 1907:39). The abundance of metates and other lithic artifacts at Las Huacas poses a serious problem for the argument that these artifacts were used as “prestige goods” and correlate to high-ranking burials, since such a quantity of metates implies that the cemetery was primarily used for an enormous “elite” population (cf. Snarskis, 1982:30). The apparent lack of “commoner” burials or burial grounds in the area suggests that this interpretation is questionable.

Without more controlled data regarding the demographic composition of the cemeteries (which currently exists only for those cemeteries which contained few metates/pendants/mace-heads), one cannot rule out age and sex as primary conditioning factors in the use of these artifact forms. Indeed, as the infant urn-burials from Vidor and Matapalo indicate, significantly different burial practices may have been used for community members based at least on age. This is not to say there were no ranked societies in Nicoya at the time, but instead that such an assertion cannot rest on the mortuary evidence from sites such as Las Huacas.

Increasing evidence is emerging that indicates the Zoned Bichrome period groups in the area lived in sedentary villages, with an economy based in part on agriculture and the extensive use of marine resources toward the end of the period (Abel-

Vidor, 1980; Lange, 1980, 1984). The nature of these settlements is still poorly known, at least in the southern Nicoya Peninsula (Guerrero, 1986; Creamer, 1986). Increased sedentism likely did correlate with increases in social differentiation within local populations. The variably known and often extensively disturbed cemeteries of the Zoned Bichrome period do not, however, provide adequate documentation of marked ranking within communities or stratified "chiefdom" societies. Perhaps, as Fonseca (1992) suggests, cemeteries like Las Huacas may represent the period of transition between "tribal-egalitarian" and "tribal-ranked" societies (cf. Creamer and Haas, 1985).

ACKNOWLEDGMENTS

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ETHNOBOTANY OF THE LOWER CHAMELECÓN MESTIZOS,
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ABSTRACT

Ethnobotanical field work among the mestizo inhabitants of the lower Chamelecón river of coastal northwest Honduras provides information on the use of 89 culturally-defined plant taxa. Data on material (food, beverages, construction, canoe-making, firewood, charcoal, medicine, etc.) and symbolic (definition of ethnic boundaries and land rights) plant use are presented and discussed. Material correlates of plant use are noted for possible application in archaeological interpretation. Considering their extensive knowledge and use of local plants, the lower Chamelecón mestizos appear to have an efficient adaptation to their environment despite the relatively short time they have lived there.

RESUMEN

Las investigaciones etnobotánicas entre los mestizos del bajo Río Chamelecón, en la costa noroeste de Honduras, proveen información acerca del uso de 89 especies de plantas reconocidas por los mestizos. Se presentan y se analizan los datos acerca de los usos: materiales (comida, bebida, construcción, embarcaciones, leña, carbón, medicina, etc.) y simbólicos (definición de límites étnicos y derechos de tierras). Se mencionan los restos y huellas materiales dejados por tales usos, para su posible aplicación en la interpretación arqueológica. Considerando su gran conocimiento y aprovechamiento de las plantas locales, los mestizos del bajo Chamelecón aparentan tener una eficaz adaptación a su ambiente pese al corto tiempo que han vivido allí.

INTRODUCTION

This report is based on data collected on the northwest coast of Honduras between August and December 1981. My aim was to study the social and material correlates of modern adaptation to a rapidly changing physical environment, in this case tropical coastal lowlands. One aspect of the project was a study of plant use by the mestizo inhabitants of the lower Chamelecón River. This paper details the results of the ethnobotanical research; the relations between plant use, landscape alteration, and social organization are discussed elsewhere (Sandweiss, ms.).

Although botanical studies often include data on local plant use in coastal northern Honduras (Dickson, 1978; Standley, 1931), these studies do not associate such use with particular socioeconomic or ethnic groups, nor is plant use approached systematically. Systematic ethnobotanical research in Honduras has been rare (e.g., Lentz, 1986 for a highland group) and has not dealt with mestizo groups. This report is an initial attempt to fill in these gaps.

In the field, I began by eliciting a list of utilized plants from informants. This list was supplemented by field observation of plant use. A total of 89 types defined by informants included 73 species of 66 genera and 41 families, and 5 unidentified plants. Although it does not cover all utilized plants, this list probably includes most of the food, canoe (*cayuco*), and construction species. Some trees used only

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for charcoal or firewood are most likely left out, and many of the medicinal plants are undoubtedly missing.

Although not the focus of this paper, one motivation for the field study was ethnoarchaeological: to gather data on the material correlates of plant use to aid in interpreting archaeological remains from the region. Readers will find a number of such correlates detailed in this report.

Environment, Inhabitants, and Informants

The study zone lies in the Caribbean coastal plain of northwest Honduras and includes the lower Chamelecón River and adjacent land, roughly between 15°50' and 15°55' north latitude and 87°45' and 87°55' west longitude (Fig. 1, 2). Much of this area lies at or within a few meters of sea level, although a number of bedrock ridges and hills punctuate the landscape. The highest of these hills, Cerro Cardona, reaches a maximum altitude of 158 m. The Chamelecón and nearby Ulua rivers meander through the broad Sula valley before discharging in the Bay of Honduras. In the past, a large sandbar existed at the mouth of the Chamelecón River, but it has been completely eroded away since a 1974 hurricane (Fifi) burst a dam on the canal which connects the Chamelecón with the larger Ulua River to the east. Most of the Ulua's discharge now exits through the Chamelecón mouth, altering the erosional regime of the latter river and causing serious problems for the local inhabitants (Sandweiss, ms.). Long-term channel migration of both rivers has left abandoned channels and associated deltas throughout the Sula valley, while the coastal study region "is made up of modern and ancient deltas" (Pope, 1984:81). The sediment of the study zone is thus "extremely fertile recent alluvium" (Carr, 1950:573), except for the hills, which generally have only shallow soils covering the bedrock.

Climate on the Caribbean coastal plain of Honduras is classified as AF (tropical rainforest climate) in the Köppen system (Carr, 1950:575). Based on data from Puerto Cortés, on the coast just west of the study zone, average annual rainfall between 1930 and 1961 was 113.8 in (ca. 787 cm), with a range of 0–5 and median of 1 consecutive dry month(s) (less than 2.4 in precipitation) per year (Johannessen, 1963:15, table 5). The annual cycle includes an autumn wet season and a spring dry season. At Lancetilla, just east of the study zone near Tela, mean monthly rainfall from 1943 to 1947 was greatest between October and December, with intermediate values for January–February and July–August, and minimum values March–June (Carr, 1950:576, fig. 3). Between 1949 and 1961, maximum and minimum temperatures recorded at Tela, on the coast just east of the study zone, were 97°F and 53°F (Johannessen, 1963:17, table 6). Mean monthly temperatures for La Ceiba (east of Tela) on the Caribbean coast from 1944–1947 show peak temperatures from May–September and minimum temperatures in December and January (Carr, 1950:574, fig. 2).

In the study zone the principal habitats (as defined by Carr, 1950:585–587) are: mangrove swamps along the coastal margins and in the Laguna de Alvarado (see Fig. 1), fresh tidal swamps near the coast and swamp forest farther inland, rainforest on higher areas, and *guamil* ("abandoned farm lands that have grown up in thickets of brush vines, and saplings" [Carr, 1950:592]). Clearings representing abandoned fields as well as those currently in use are easily seen on aerial photographs (Fig. 2). Corozo palms (*Attalea cohune*) are abundant in most of these fields and are the only large plants left standing through all phases of field preparation, cultivation, and abandonment. Corozo palms generally do not occur in

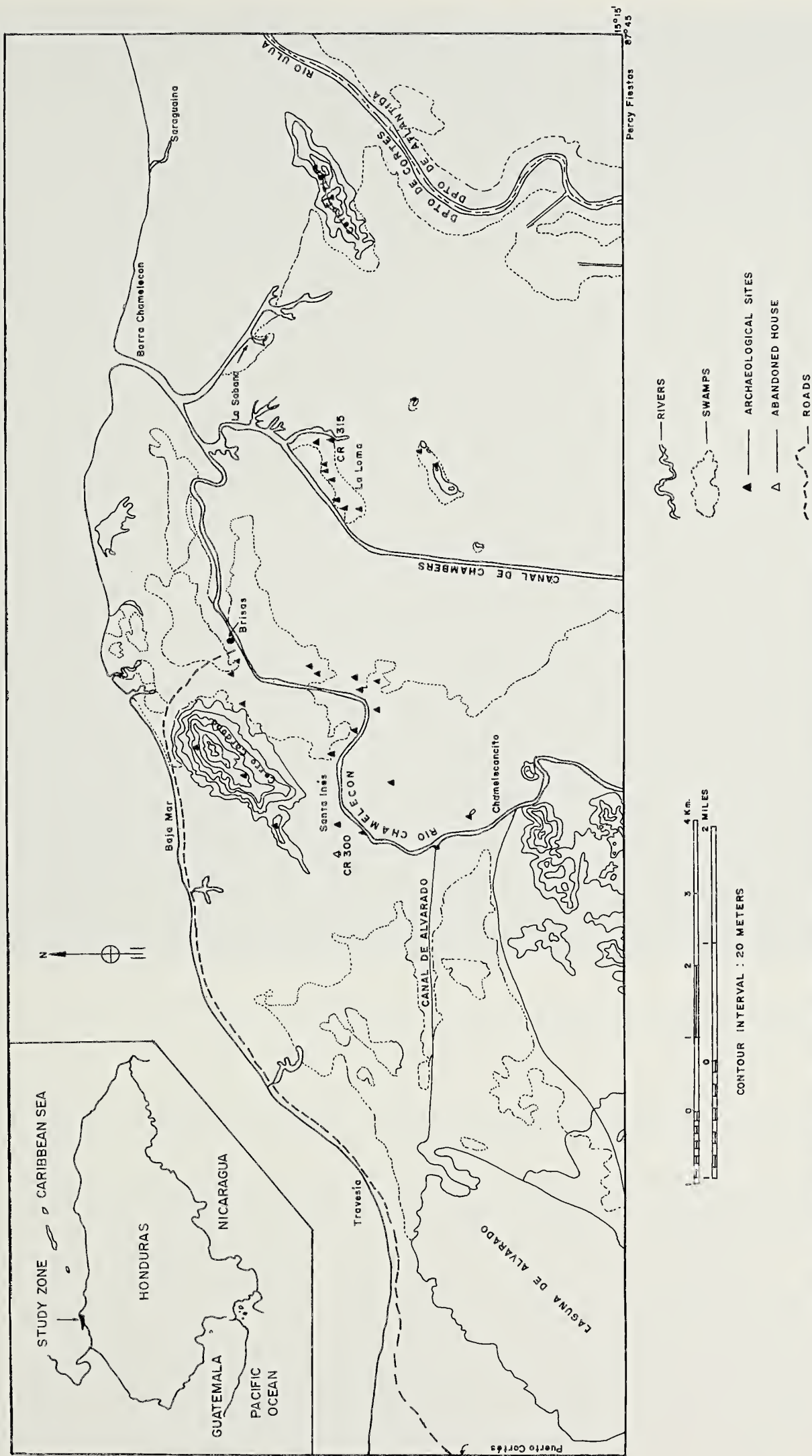


Fig. 1.—Map of the lower Chamelecón area, showing geographic features, modern communities, and archaeological sites.



Fig. 2.—Aerial photograph of the study zone near the mouth of the Chamelecón River, which can be seen in the upper center of the photo.

fields cleared for pasturage, but they may be present in clearings around homesteads.

In precolumbian times, a group known as the Jicaque occupied the Caribbean coastal plain of Honduras in the vicinity of the lower Chamelecón and Ulua rivers (Johnson, 1948:map 5), which includes the area covered by this study. In the 16th century, the Jicaque abandoned the coastal region for higher regions farther inland, where they were safer from Spanish persecution; today they live on a reservation in the uplands of central Honduras (Lentz, 1986). The modern inhabitants of the lower Chamelecón are mostly Spanish-speaking *mestizos*, the descendants of several families from the highlands who emigrated to the area at the beginning of this century. There are also two families of *Belizeños* who arrived from Belize (former British Honduras) at the same time or a bit earlier than the *mestizos*. Both of these groups have now been in the area for about 85 years. The *Belizeños*,

many of whom speak English as well as Spanish, have intermarried with the mestizos. Since the extension of the road from Puerto Cortés around Cerro Cardona to the new community of Brisas, there has been a small influx of coastal mestizos, mainly from around the Ulua delta. All of these people are primarily farmers, although some livestock is raised in the area. They also fish, hunt, and gather wild plants.

Several Garifuna, or Black Carib, villages are in the same general area but away from the river. The Garifuna are descended from escaped African slaves and native inhabitants of the island of Saint Vincent. Forced to migrate off that island, they settled the Bay Islands of Honduras and established communities along the Caribbean coast from Belize to Nicaragua. Black Caribs have been on the Honduran coast for over 200 years (Gonzalez, 1969). In the study area, two Garifuna communities (Baja Mar and Travesía) lie to the west of Cerro Cardona; a third Garifuna settlement (Saraguaina) is located to the east of Barra Chamelecón, a mestizo village at the river mouth (Fig. 1). The Black Caribs are a maritime-oriented group which is racially, culturally, and linguistically distinct from the lower Chamelecón mestizos. The Black Caribs live in separate settlements away from the river and the mestizo villages and homesteads, although some Black Caribs do have land rights in the river zone. Inter-marriage between Garifunas and mestizos is rare, although frequent contact takes place as the mestizos and the Black Caribs move through the region.

The treatment of the bitter variety of manioc (*Manihot esculenta*, see Appendix) is an example of the cultural differences between these two groups. The Garifuna use the *culebra* (snake) and sifter method to detoxify and prepare bitter manioc. (The snake and its use are identical to the *tipiti* of the Amazonian region, see for instance Lowie, 1948:6.) The resulting flour is used to make *cassave*, an unleavened, sheetlike bread. This method of processing is common among indigenous groups throughout the lowlands of tropical America and was probably passed down to the Garifuna by their indigenous island ancestors. The mestizos, on the other hand, know how to process bitter yuca, but claim that they rarely grow this plant and have no need for the processing techniques or equipment. Several informants stated explicitly that cassave was a Black Carib food. I never saw a *culebra* or sifter in a mestizo house, and cassave was always made and sold by Garifuna women.

My principal informant was a 40-year-old male mestizo from the community of Brisas, who was a native of La Sabana and a life-long resident of the study zone. Farmer, canoe-maker, and jack-of-all trades, he had extensive knowledge of local plants, animals, and people, and of the material technology and social organization which integrate them. Field observations usually confirmed the accuracy of information received from this informant. Interviews were carried out in the presence of one to ten other local inhabitants, who offered comments or added information when pertinent. Finally, much of the information on plant use was gathered or confirmed during the six months of field work in the communities of Brisas and Barra Chamelecón.

The presence of other people during the interviews may have altered the responses which I received from my principal informant. However, the kinds of questions asked were generally technical and concerned with knowledge in the public sphere, and did not seem to be considered threatening. In any case, almost all of the information was field-checked and shown to be accurate. The only area in which the answers were probably restricted was in reference to magical uses of plants, a subject only briefly discussed in this report.

For each taxon defined by informants, the data elicited included common name, description, habitat, seasonality of the utilized plant part(s), collection or production technology, uses, and whether or not the plant is considered wild or cultivated. The Appendix summarizes the data on mestizo plant use for each taxon.

Agriculture

Agriculture in the study zone is of the swidden, or slash-and-burn variety. Fields are prepared by cutting the vegetation, leaving it to die and dry, and then burning it. Seeds or vegetative cuttings are placed in holes made with a *barreta*, a pointed stick about two cm in diameter. The species being planted determines the spacing of the holes and therefore the time required for planting. Fields are measured in *manzanas*, a Spanish unit originally related to the size of the royal apple orchards and now equal to about a quarter acre. Weeding must be done at least once during the growing season; formerly, the people in the study zone used machetes to weed by hand, spending up to two weeks per manzana. Today, herbicides are used almost exclusively, as they are inexpensive and require less than a day to cover the same area. The only crop for which herbicides cannot be used is beans (*Phaseolus vulgaris* and one unidentified), which are susceptible to the herbicidal poison. My principal informant first used herbicides in 1962. Neither fertilizers nor insecticides are used in the area, and insect pests do not seem to be a problem.

Settlement Pattern

The mestizo population of the study zone is distributed primarily along the river, which is the main avenue of transit. The recent extension of the Puerto Cortés road from Cerro Cardona to the Chamelecón River is being settled in the same way as the river. Two patterns prevail: isolated homesteads and small nucleated villages. The homesteads are spaced several hundred meters apart along the river and occur with less frequency on the hills. La Sabana with about 35 households is both the largest and the most nucleated village. At the river mouth, the village of Barra Chamelecón extends east parallel to the shoreline. As the distance from the river increases, so does the distance between houses.

Swidden agriculture requires that fields be rotated periodically, yet most homesteads do not shift location. This situation is due in part to the small size of the local population relative to the amount of available agricultural land, but it is also related to the high degree of mobility imparted by the river. The mestizo farmers can generally reach their fields in less than two hours. Of the few abandoned homesteads that I observed or was told about, all were on hills and none were directly on the banks of the river. One of the abandoned houses was on Cerro El Tigre, which is one of the few plots of agricultural land more than two hours travel from the river.

CONTEMPORARY PLANT USE

Plants serve a variety of functions in the study zone (*see* Appendix). Plant material is used for food, beverages, construction, canoe-making, firewood, charcoal, medicine, and a number of other purposes. Plants also have several symbolic roles in the region. First, the differences between the local groups in selection and use of plants reflect cultural boundaries and distinct historical traditions. Second, in situ cultivated plants define rights in land. According to local tradition, a person does not (in most cases) own land per se, but instead has exclusive rights to the

products of plants which he or she has cultivated. Perennial, persistently producing cultigens—usually fruit trees—are therefore of much greater value for maintaining land rights than are annual, short-term crops. Coconut palms (*Cocos nucifera*) are particularly valued for their long productive life as well as for their importance as a source of oil. The maintenance of rights in land through cultivation of fruit trees is known from other parts of Mesoamerica. Millon (1955) has suggested that it has cultural-evolutionary significance in the development of private property in this part of the world.

While investigating a recently abandoned house on a low ridge between the Chamelecón River and Cerro Cardona (Fig. 1: site CR-300), I made an inventory of the plants locally classified as useful growing within a 20-meter radius of the house center. Of a total of 376 individual plants, all of which produce edible parts, 33% were sweet yuca (manioc, *Manihot esculenta*), 33% pineapple (*Ananas comosus*), and 13% sugar cane (*Saccharum officinarum*). All three of these species are short-duration crops of economic importance in the region. Virtually all of the yuca grew in a garden behind the house site, while most of the pineapple was planted to the east and south of the house. In both cases, deliberate cultivation for mass harvesting was apparent and confirmed by informants.

Of the remaining 84 plants, 74 were fruit trees (ten species, including coconut palms), of which three fourths were saplings. These trees grew on all sides of the house site, and their presence suggested that the former occupant was concerned with maintaining control over that plot of land. He had burned down the house when he abandoned it, presumably to prevent reoccupation by squatters.

Wild Versus Cultivated

My informants had very clear ideas about which plants are wild and which are cultivated. Of the taxa on which I collected information, about half fall into each category. In addition, three trees are said to grow both wild and as cultigens. Two of these are fruit trees and one is *guanacaste* (*Enterolobium cyclocarpum*), an important source of lumber. In all three cases, the wild plants are considered escaped cultigens.

The principal criterion for deciding the status of a plant appears to be whether it is currently planted or would be planted if mature specimens were scarce. If a cultivated plant species loses importance, or for some other reason is no longer planted, it presumably changes status. For example, the corozo palm is now classified as wild. In the past, the people of the study zone extracted oil from corozo nuts, and up until 16 years ago, a factory bought these nuts to produce oil, soap, and candles. Given the wide distribution of this palm in swidden fields and around homesteads, it is likely that corozos were formerly encouraged, if not cultivated, along the lower Chamelecón and were formerly considered as cultigens.

Classification as wild has a significant impact on the ways a plant is used. Wild species cannot confer rights in land. Perhaps for this reason, wild trees are cut down for firewood or charcoal even when they produce marketable fruit, as in the case of the nance (*Byrsonima crassifolia*). In relation to cutting these fruit-bearing species, informants stated specifically that the loss of future harvests does not matter because the trees are classified as wild. The fact that destruction (through use) of a wild plant cannot engender property disputes may help explain this attitude.

Either wild or cultivated plants tend to dominate each category of plant use discussed in the following sections. The majority of consumed plants (food and

beverage) are cultivated, while nearly all of the construction species (houses and canoes) as well as the destruction species (firewood and charcoal) are wild. Only the medicinal plants are more or less evenly divided between the two statuses. The predominance of cultigens among the consumed species reflects the importance of agriculture in the lives of the people I studied. In contrast, most of their animal foods come from wild species that are fished, gathered, or hunted.

Food

The people of the study zone are self-sufficient in basic foods: they grow, fish, herd, hunt, or gather almost everything they eat. Plants are basic to the diet, and my list includes 46 edible species (Appendix). The principal commercial crops are rice (*Oryza sativa*), which is grown on low ground along the river, and maize (*Zea mays*), which is planted on the hills, ridges, and other well-drained areas. Red and black beans (*Phaseolus vulgaris*) and "face" beans (*frijol de carita*, unidentified Fabaceae) are marketed occasionally, as are pineapples (*Ananas sativas*), some *Citrus* fruits, and a few other plant products.

Among the crops cultivated exclusively for home consumption, sweet yuca (*Manihot esculenta*) is most important and constitutes the bulk of the plant foods locally consumed. Sweet potatoes (*Ipomoea batatas*) are also eaten frequently. Both of these species can be planted at any time of year, and have tubers which remain edible in the ground for several months or more after they reach maturity. Consequently, yuca and sweet potatoes can be harvested as needed throughout the year. Most of the other cultigens ripen simultaneously, require rapid harvesting, and produce two or sometimes three crops per year.

Eleven of the food plants on the list are considered wild. Most of these are fruit trees, and several other fruit trees such as mango (*Mangifera indica*), a native of Southeast Asia, are said to escape from cultivation and grow wild. The wild plant foods tend to be seasonal and generally of little caloric importance in the diet.

Although storage of dried grains such as rice and maize is possible, I observed few cases of storage at the household level. Presumably the wet, hot climate makes long-term preservation difficult given the general absence of water- and pest-proof granaries. Both rice and maize are eaten at harvest time, and small amounts are occasionally kept for later use. In Barra Chamelecón, I saw two cane-and-thatch huts used to store *quintal* (100 lb) sacks of corn for short periods prior to transportation to the market in Puerto Cortés. Both of these buildings are located at a boat landing on the river bank. In Brisas, at the end of the road from Puerto Cortés, the single concrete-floored house serves as a collection point for quintales of rice (and to a lesser extent maize) in transit to the market.

Beverages

Despite the fact that carbonated beverages, beer, and commercial *guaro* (a liquor) are frequently available, I recorded the use of 21 plant species in the preparation of a variety of beverages. These drinks fall into several categories, including teas, fruit juices, fermented juices, distillates, and hot drinks made from ground and roasted seeds. Coffee beans (*Coffea arabica*), cacao beans (*Theobroma cacao*), and maize kernels are used in the latter fashion to make coffee, chocolate, and *piñol* and *atol* (sweet drinks). Boiled in water, both the leaves and fruits of the allspice tree (*Pimenta officinalis*) brew a palatable tea.

Most of the tree fruits, both wild and cultivated, are made into juices by squeezing or soaking in water and adding sugar. The juice is often allowed to ferment

into wine. Both corn kernels and rice grains may be soaked in water and mixed with sugar, then either drunk fresh, fermented to produce *chicha* (a sort of beer), or further distilled into a type of guaro. Beer vine (*Gouania polygama*) and ginger root (*Hedychium coronatum*) are pounded, boiled together in water, and fermented with sugar to make ginger beer.

House Construction

Most of the people along the lower Chamelecón build their houses of locally occurring plant materials. All but one of the species mentioned in connection with local construction are considered wild, although two cultivated species are sold to the sawmill. The resulting lumber is rarely used in the study zone.

House building involves four kinds of plant material. Trunks of immature trees (ten cm or less maximum diameter) form the frame. The leaves of the corozo palm, or in its absence the stalks of guinea grass (*Panicum maximum*), serve as thatch. Parallel rows of cane stalks (*Gynerium sagittatum*) form the walls, although occasionally slats cut from the outer trunk of the yagua palm (*Roystonea oleracea*) are nailed or tied to the frame to make a more substantial wall. Floors are generally of dirt, but a few houses have poured concrete floors. Most people build on hills or small rises; houses in swampy areas must be put on stilts made of tree trunks and floored with yagua strips or imported planks.

Homesteads usually consist of two large, separate structures—the house proper and the kitchen. Smaller buildings made of the same materials serve as pigsties or hencoops, while intermediate-sized buildings are sometimes built for storage. Outhouses are very rare.

Doors and windows are generally left open or covered with cloth. Wooden doors or shutters occur rarely. Inside the house, cane walls subdivide the space into sleeping and general purpose rooms. The kitchen consists of a room with an *horno* (oven/stove) in one corner. Hornos are made of a cane frame plastered over with *adobe* (mud), sometimes set on wooden legs.

The abandoned house at CR-300 (see above) had been built with a pole frame, cane walls, and a thatched roof. Some of the joints were apparently secured with nails, as I found several nails on the floor. A charred piece of the wall showed that vine lashing was also used. The remains of the horno yielded chunks of cane-impressed baked mud identical to the material referred to as *bajarreque* by archaeologists and generally interpreted as evidence of wattle-and-daub walls when other contextual data are lacking or equivocal.

Canoe-Making

Canoes, called *cayucos* in the study zone, are vital to the local economy. They provide transportation from homestead or village to neighbors, fields, and the market. Much of the land near the river is impassable, so people, crops, building materials, firewood, charcoal, and manufactured goods must all move through the study zone in cayucos. Watercraft allow large quantities to be moved rapidly and with a minimum of effort. Cayucos are made by the mestizo men, and the techniques of manufacture are passed down from father to son. Certain people are known for their skill in canoe-making; my principal informant was one of these men. He learned from his father, who in turn learned from his father, who was one of the *primitivos* (first settlers and founders of the major local families). I could not determine whether the *primitivos* brought the knowledge of cayuco construction with them from the highlands, learned it from someone on the coast,

Table 1.—*Ranking of local woods in order of preference for canoe-making by principal informant, 1 November 1981.*

1st rank:	Cedro (<i>Cedrela mexicana</i>), Guataúl (unidentified)
2nd rank:	Santamaría (<i>Calophyllum rekoï</i>), Guanacaste (<i>Enterolobium cyclocarpum</i>), San Juan (<i>Cy-bistax donnell-smithii</i>)
3rd rank:	Carao (<i>Cassia grandis</i>), Nargosta (<i>Terminalia catappa</i>), Macueliz (<i>Tabebuia rosea</i>)
4th rank:	Zapotón (<i>Pachira aquatica</i>), Ceiba (<i>Ceiba pentandra</i>)
Woods used but not ranked:	Aguacatillo (<i>Nectandra</i> sp.), Chiniquite (<i>Bursera simaruba</i>), Mango (<i>Mangifera indica</i>), Mazapán (<i>Artocarpus altilis</i>), Sauce (<i>Salix chilensis</i>), Zapote (<i>Calocarpum mammosum</i>)

or reinvented it. However, the most likely of these possibilities is learning from other coastal zone inhabitants.

My list includes 16 tree species used for canoe-making, of which 12 are wild, two are cultivated, and two can be either wild or cultivated. Factors influencing the choice of wood for a particular cayuco include the availability and location of the tree, the speed with which the boat is required, the use for which it is intended, the projected size, the amount of time available to the builder, and most importantly, the durability of the wood. Different tree species produce canoes of varying durability; those which last longest are generally the hardest to work. Table 1 shows my principal informant's ranking of local woods in order of preference for canoe-making.

Each cayuco is made from a single trunk. The process of manufacturing takes place at the tree's living site. After the trunk is cut down and laid horizontally, the top third is planed off with an axe or adze. The outline of the canoe is marked with charcoal on the flat surface (Fig. 3, top) and the interior is excavated with iron axes or adzes. Charring does not take place at any stage of the process. Shaping the exterior, again with an axe and adze, constitutes the final step unless an outboard motor is to be used. In that case, the builder starts with a large trunk and later adds strakes to the sides and a platform for the motor on the stern. I counted only five outboards in the study zone.

The basic design variable taken into consideration by the cayuco builder is the length/width ratio. Variation is achieved by varying the relative lengths of the *desagues* (the mirror-image, tapered bow and stern sections) and the *centro* (the straight-sided central section) (Fig. 3, bottom). Greater relative length means greater speed, while greater relative width increases both stability and cargo capacity. The intended use of the boat determines the length/width ratio chosen by the builder.

Firewood and Charcoal

Virtually any deadwood is burned as firewood, but not every kind is suitable for charcoal-making. Of the 29 species mentioned as firewood (unlikely to be an exhaustive list), over a third were specifically indicated as unsuitable for charcoal. Just under half of the trees are cut directly for burning; predictably, all eight of the cultivated plants on the list are burned only when dead or when wood is left over from some manufacturing or construction process. As noted above, live wild fruit trees may be cut for burning, while cultivated trees may not.

The people of the study zone collect firewood daily for home use, and at least one man makes his living cutting wood in the swamp and selling it upriver in

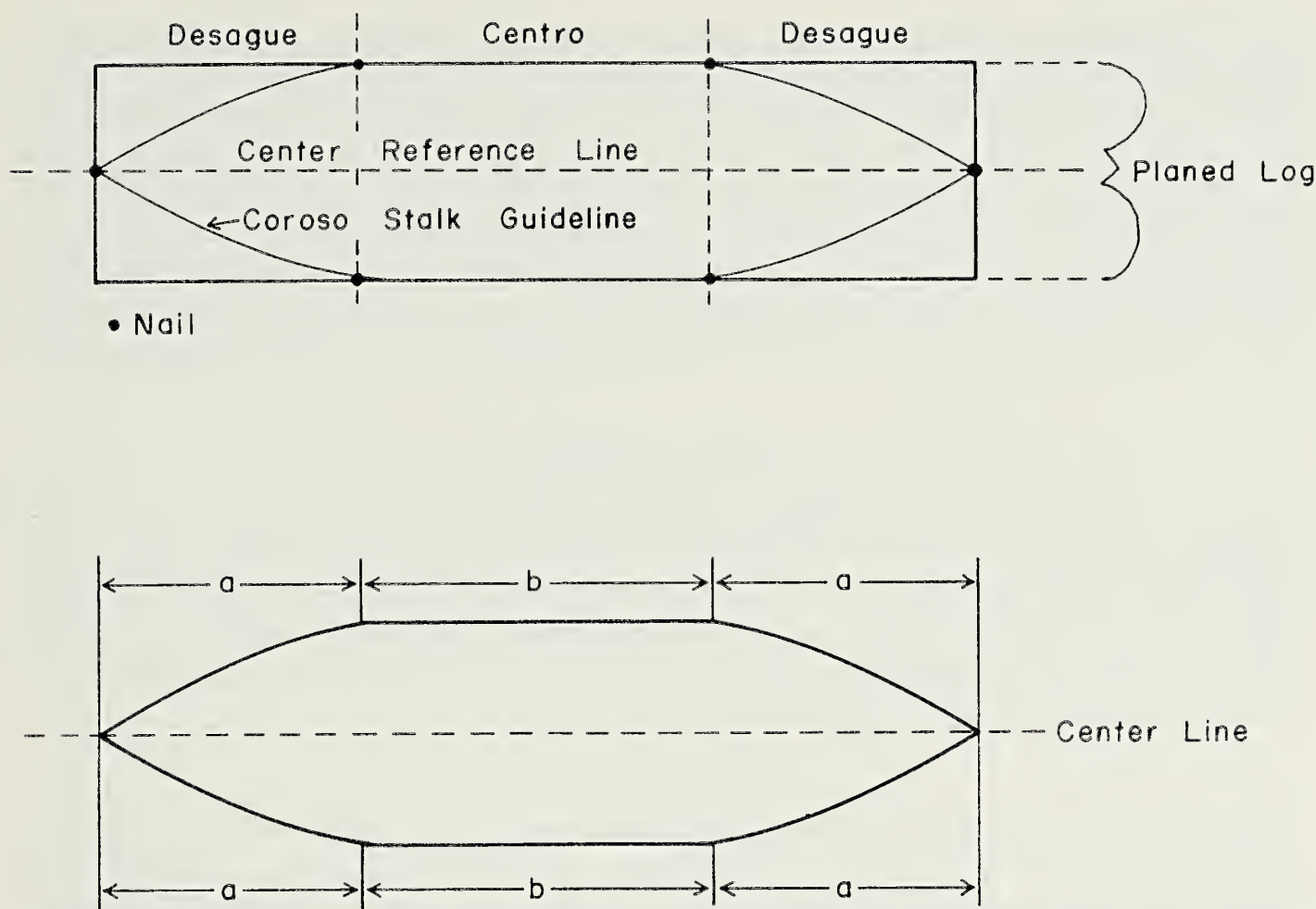


Fig. 3.—Schematic drawings of a *cayuco* (canoe). Top shows where nails are placed on a planed tree trunk to draw the center reference line and, using bent corozo (*Attalea cohune*) stalks, the outlines of the bow and stern. Bottom shows the relative dimensions of a *cayuco*: all “a’s” are of equal length, as are the “b’s”; *cayucos* with different qualities for different uses are made by varying the ratio between a and b. Based on field observations and drawings done under informants’ supervision.

Chameleconcito (Fig. 1). Charcoal is not used locally but is sold in Puerto Cortés. Any family that wants to raise small amounts of cash can make charcoal. The process involves clearing a circle of earth about ten m in diameter, stacking the wood in a cone, covering it with grass and then dirt, leaving holes on the sides and bottom, and igniting the wood. After three days of smoldering, the dirt is removed and the charcoal raked out over the whole circle. Pieces which continue to burn are doused in water before the charcoal is bagged. Each family uses the same circle each time they make charcoal. Through time, the circles are depressed and permeated with charcoal dust, resulting in a blackened, circular floor sunk several centimeters or more below the surrounding ground.

Medicine

My list includes 29 species used medicinally, of which 16 are cultivated. Many more plants are undoubtedly considered to have curative value, but none of my informants was a specialist in herbal medicine and I was unable to interview the only local *curandera* (healer), an old woman living in Santa Inés. The listed taxa are said to cure a wide variety of ailments, ranging from constipation to unwanted pregnancies (see Appendix).

Preparation of most of the medicines involves soaking or brewing leaves, bark, or roots in water. The resulting potion is not always drunk; for instance, a brew made from *ipacina* roots (*Petivera alliacea*) is warmed and used to bathe the head to relieve colds. The same liquid, if drunk, is said to cure stomachaches and to

cause an abortion. Not all medicines are prepared by soaking or boiling in water. The *jícara* flower (*Crescentia cujete*) is heated until it sweats and is then put in the ear to relieve earaches. Sniffing the sap of the *vivorán* stalk (*Asclepias curassivaca*) causes sneezing to clear a stuffy nose. In the case of *chiniquite* or *indio desnudo* (*Bursera simaruba*), the use of sympathetic magic is apparent. If a child is born with a navel that protrudes several centimeters because of a hernia, a hole is cut in the bark of a chiniquite tree. First the child's navel and then one of the big toes are placed in the hole. Informants say that as the bark grows over the hole in the tree, the child's stomach will simultaneously consume the protruding navel.

Some plant preparations are used for purposes not directly related to curing. Boiled in water, *valeriana* roots (*Vetiveria zizanoides*) or avocado leaves (*Persea americana*) produce an "intelligence potion" said to make a person smarter. Hot peppers (*Capsicum frutescens*), ginger root (*Hedychium coronatum*), and a brew made from *chiniquite* bark are all supposed to act as sexual stimulants. The fruit of the rose apple tree (*Eugenia jambos*) is supposed to be poisonous in conjunction with alcohol; my principal informant suffered a swollen abdomen, nausea, and vomiting from such a combination.

Other Uses

In addition to the major categories already discussed, plants serve a variety of other functions in the study zone. Six trees are said to produce good wood for furniture-making, and other species are probably used as well. Pieces such as beds, chairs, and tables are made with a saw, hammer, and nails. Large, utilitarian artifacts such as mortars (up to a meter high and a half meter across) and *bateas* (large, rimmed wooden trays for kneading dough, coconut pulp, etc.) are cut and carved from the same trees used for canoe-making. Cutting a *jícara* (tree gourd, *Crescentia cujete*) in half along the long axis and scraping the rind clean creates two large, oblong bowls known as *guacales*. Guacales can also be made from either gourd or squash varieties of *Cucurbita pepo*. Guacales serve primarily as water vessels for drinking and as receptacles for animal feed and water. If the *jícara* fruit is placed on end and the top third removed, the resulting vessel is called a *cumba*. Several holes are drilled in the rind to attach a cord, and farmers tie *cumbas* to their waists to hold seed during planting.

Although several trees (mostly wild) are suitable for fenceposts, informants consistently stated a preference for those species such as *zapotón* (*Pachira aquatica*) which take root and become live trees. According to informants, *zapotón* grows in swampy ground; of the other two fenceposts species which take root, *macueliz* (*Tabebuia rosea*) will grow everywhere and *sauce* (*Salix chilensis*) lives on level ground, swampy or dry.

In the past, the bark of the red mangrove (*Rhizophora mangle*) was soaked in water to get a reddish liquid used for tanning leather. The last remembered collection of mangrove bark was around 1954, when the local inhabitants still sold the bark in the port of Tela, east of the study zone.

Through the mid-1960s, a factory in Puerto Cortés bought corozo palm nuts to make oil, soap, and candles. Locally, the oil was burned for light and used in cooking in the same way coconut oil is used today. The nuts were opened by placing them on a large, soft rock and hitting them with another stone. By consistently placing the nuts on the same part of the anvil stone, a hole gradually formed. At first, this hole helped the cracking by holding the nut in place; after the pit became too deep, a new position on the anvil was chosen and the process

repeated. I have seen “corozo stones” with several egg-shaped pits on each of two or more sides. Since they lost their commercial value, corozo nuts have rarely been collected. The only use which I observed was burning to provide an insect-repelling smudge.

The people of the lower Chamelecón accomplish most of their personal cleansing by scrubbing with dried *paste* fruits (*Luffa cylindrica*). To prepare a luffa, the skin is peeled from the fruit, the seeds thrown out, and the remaining material washed with water and dried. Paste is cultivated in the study zone; one plant grew on top of the abandoned house at CR-300.

DISCUSSION

Although their ancestors arrived from the highlands only three or four generations ago, the mestizos of the lower Chamelecón have developed an efficient adaptation to the coastal environment. This environment consists of swamps and low hills covered with tropical rainforest and cut by the river and its distributaries. The area is radically different from the highland Comayagua Valley where most of the families have their origin. How or from whom these people learned to manipulate the resources and geography of the coastal lowlands is still open to speculation: informants were unclear on this point. Perhaps the Belizeños brought the necessary knowledge from Belize and taught it to their neighbors and kinsmen-to-be. Maybe the primitivos (first mestizo settlers) learned from the Garifuna, although relations between these groups today and in the remembered past argue against this possibility. The eldest surviving son of one of the founders of Barra Chamelecón told me that when his father arrived in the area, the Garifuna spoke no Spanish and tended to resist contact with the mestizos. Whether strictly true or not, this statement indicates an attitude of social distance supported by other data such as the differential use of *cassave*. Furthermore, the Garifuna adaptation is primarily maritime, in contrast to the riverine adaptation of the mestizos. The two groups continue to maintain social as well as geographic distance. The remaining possibility is that in the last 85 years or so, the primitivos and their descendants have discovered for themselves, by trial and error, the extensive knowledge of their environment which they now display. Most likely, some combination of these possibilities accounts for the mestizos' local environmental knowledge.

The mestizo study group demonstrates dynamic flexibility in adapting to new elements. Sometimes old models are applied to new situations, as in the case of the new road from Puerto Cortés to Brisas. The road provides easy access to the port in the same way as does the river, and settlement along the road is being established according to the pattern originally used along the river.

In other cases, the mestizos have incorporated new elements involving different forms of manipulation. When the primitivos came down from the highlands, they must have been familiar with maize and beans, but yuca and rice do not grow in the highlands and so must have been acquired on the coast. Today, yuca is the principal vegetable component of the local diet, while rice is grown in greater quantity than any other crop and accounts for the largest part of the cash income. Rice farming, in particular, is different from growing the crops typical of the highlands. The decision to concentrate on rice as the principal commercial crop makes perfect economic sense in terms of return on labor investment; moreover, rice occupies a niche (swampy ground) previously unexploited in the area. The data in Table 2 suggest the reasons why maize occupies second place and beans

Table 2.—Comparative data for beans, maize, and rice crops in the lower Chamelecón region. * If a maize field is left in fallow for only 3–4 years, it can be planted again but will yield only one crop.

	Beans (<i>Phaseolus vulgaris</i>)	Maize (<i>Zea mays</i>)	Rice (<i>Oryza sativa</i>)
Yield (quintales/manzana)	40–45	up to 60	up to 80
Sale price (lempiras/quintal)	50–100	16–30	up to 80
Crops/Year	1	2–3	3
Number of consecutive years can crop	4–5	1	3
Years in fallow	2–3	6–10*	6–8
Time required to plant 1 manzana	12–15 days	4–6 days	12–15 days
Use herbicide to weed	No	Yes	Yes
Time required to weed	15 days	1 day	1 day

a distant third in terms of area (number of manzanas) devoted to each of these crops.

The importance of plants in the daily life of the lower Chamelecón mestizos goes beyond the material categories related to subsistence (broadly defined) and health. Plants define land rights and cultural boundaries.

CONCLUSION

The study of plant use along the lower Chamelecón River offers a means of demonstrating the depth and efficiency of the modern adaptation to this coastal lowland environment. Plants provide food to eat, heat with which to cook, drinks for all occasions, shelter against tropical storms, cures for every ailment, transportation throughout the area, and cash for the other necessities as well as the luxuries of life.

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APPENDIX

Lower Chamelecón mestizo plant use by taxon. Terms in boldface are local names for the plant; English names (where known) are listed in parentheses following the local name. Botanical data are from Dickson (1978, personal communication, 1981), Standley (1931), and personal observation (1981). Plants are native to the region unless otherwise noted. Wild/cultivated in this Appendix is the cultural classification by lower Chamelecón mestizo informants. All data on plant use are from the local informants unless otherwise noted.

Anacardiaceae

Mangifera indica L. **mango**. (Dickson, 1978:54; Standley, 1931:259). Cultivated tree, introduced from Southeast Asia. Fruit eaten, squeezed for juice, made into jam. Trunk used to make *cayucos* (dugout canoes). Tea made from leaves and sugar used to relieve coughing.

Annonaceae

Annona muricata L. **guanabana** (soursop). (Dickson, 1978:15; Standley, 1931:195). Cultivated native tree. Fruit eaten or made into juice. Dead trees used for firewood, not good for charcoal. Standley noted that it was “sometimes found half-wild around the sites of former dwellings.”

Apiaceae [=Umbelliferae]

Eryngium foetida L. **culantro**. (Standley, 1931:313–314). Low glabrous perennial herb. Wild. Used as a condiment in cooking, or eaten raw. When babies or young children have “*aito*” (when they eat something which makes them want to drink but not eat), the stomach is massaged to get out the “*mal*” (badness, illness), then whenever they ask for water they are given an infusion of *culantro* roots to assuage their thirst and inspire hunger.

Araceae

Philodendron sp. **canculuncu**. (Standley, 1931:122). Large, epiphytic vines. Wild. Used for lashing in house construction; peeled, the vine is used in handicrafts such as baskets, hats, bags.

Arecaceae [=Palmae]

Attalea cohune Mart. [*Orbignya cohune* (Mart.) Dahlgren] **corozo** (manaca or cohune palm). (Dickson, 1978:18; Standley, 1931:110–111). Tall palm. Wild. Leaves used for roof thatch. Nuts formerly (up to ca. 1965) sold to local factory for soap, candles, oil. Oil also extracted from nuts in the past by cracking seed case on special cutting stone, then grinding flesh in wooden mortar; water was added to make “*chingaste*,” which was cooked and strained to extract oil. Corozo oil was used in same way as coconut (*Cocos nucifera*) oil: for cooking, drunk as laxative. At time of study, only active use of corozo nuts was burning them whole as a smudge to drive off mosquitoes.

Cocos nucifera L. **coco** (coconut). (Dickson, 1978:32; Standley, 1931:114). Tall palm. Cultivated. Coconut milk is drunk; flesh is eaten or processed to extract oil: flesh is grated, water is added to make “*chingaste*,” which is pressed to extract liquid; this liquid is left overnight in a covered container then strained; resulting solids are heated and restrained through cloth to get the oil. Coconut oil is the principal cooking oil in the study area. Both the milk and the oil can be taken as laxatives.

Roystonea [*Oreodoxa*] *oleracea* Mart. **yagua** (royal palm). (Standley, 1931:116–117). Very tall palm. Wild. Trunks of mature trees used as houseposts. Sections of outer trunk used as natural planks for house walls and floors. *Palmito* (palm hearts) eaten raw or cooked.

Asclepiadaceae

Asclepis curassivaca L. **vivorán**. (Standley, 1931:324). An erect herb. Wild. Cotton soaked in sap is held to nose to cause sneezing and thus relieve stuffy nose.

Avicenniaceae

Avicennia nitida Jacq. **mangle negro** (black mangrove). (Standley, 1931:334). Mangrove tree. Wild. Wood used for house frames and as firewood.

Bignoniaceae

Crescentia cujete L. **jícara** (calabash tree). (Standley, 1931:353–354). Small, cultivated tree, apparently not native. Dried fruit rinds used as containers such as *guacal* (bowl) and *cumba* (holder for seeds during sowing). Wood used as firewood. Flower heated on griddle and placed in ear to relieve earache.

Cybistax donnell-smithii (Rose) Seibert [*Tabebuia donnell-smithii* Rose] **San Juan**. (Dickson, 1978:35; Standley, 1931:356). Tall, wild tree. Wood used for frames in house construction and for furniture-making. Trunk used for making *cayucos*. Leftover wood pieces from construction or canoe-making used for firewood and charcoal.

Tabebuia rosea (Bertol.) DC. [*T. pentaphylla* (L.) Hemsl.] **macueliz**. (Dickson, 1978:71; Standley, 1931:356–357). Wild tree. Trunk used for *cayuco* construction; wood used for house frames. Leftover pieces of wood burned for firewood or charcoal. Planted to create living fence.

Bombacaceae

Ceiba pentandra (L.) Gaertn. **ceiba** (kapok tree). (Dickson, 1978:28; Standley, 1931:276–277). Giant tree. Wild. Trunk used for *cayuco* construction; wood used for furniture. Leftover pieces of wood used for firewood; not good for charcoal.

Pachira aquatica Aubl. **zapotón** (provision tree). (Standley, 1931:278). Small tree, common in swamps. Wild. Used for *cayuco* construction. Planted to create living fence. Bark soaked in water for a day and drunk for kidney problems or lower back pain.

Bromeliaceae

Ananas comosus (L.) Merr. [*Ananas sativas* Schult.] **piña** (pineapple). (Standley, 1931:126–127). Probably a native of Brazil. Cultivated. Fruit is eaten raw, used in baked goods, made into juice, or fermented with water and sugar to make wine. Basal surrounding leaves are pounded and used as a poultice on broken bones or dislocated joints.

Burseraceae

Bursera simaruba (L.) Sarg. **chinacuite**, **indio desnudo** (gumbolimbo, torchwood). (Dickson, 1978:23; Standley, 1931:238–239). Small or large tree. Wild. Trunk used for *cayuco* construction. Planted to create living fence, or cut when young for fenceposts. When children are born with an abdominal hernia, a hole is cut in the bark of a *chinacuite* tree; the child is lifted to the hole and his or her protruding navel is stuck in the hole, then the big toe of one foot is struck in the hole. The hernia is supposed to heal as the bark grows over the hole through time. An decoction of *chinacuite* bark is said to augment sexual potency.

Chrysobalanaceae [=Rosaceae]

Chrysobalanus icaco L. **jicaco** (coco plum). (Dickson, 1978:29; Standley, 1931:205–206). Shrub or very small tree, common on beaches. Fruit eaten raw.

Clusiaceae [=Guttiferae]

Calophyllum reko Standl. **Santa María**. (Standley, 1931:285–286). Tree, can be very large. Wild. Trunk used for *cayuco* construction. When young, trunk can be used for house construction. Wood used for furniture. Leftover pieces good for charcoal or firewood.

Combretaceae

Laguncularia racemosa (L.) Gaertn. **mangle blanco** (white mangrove). (Standley, 1931:301). Shrub or small tree, grows in mangrove swamps. Wood used for house construction and firewood.

Terminalia catappa L. **nargosta** (Indian almond). (Dickson, 1978:72; Standley, 1931:301). Medium-sized tree. Native of Old World tropics. Standley noted *T. catappa* planted for shade as well as “growing half-wild in thickets, probably on the sites of former dwellings.” Trunk used for *cayuco* construction. Cut for charcoal when small, also used for firewood.

Convolvulaceae

Ipomoea batatas (L.) Lam. **camote** (sweet potato). (Standley, 1931:326). Creeping herbaceous vine. Cultivated for the edible tuber. Cooked and eaten plain or made into bread, sweets, or drink. Not commercialized.

Cucurbitaceae

Cucurbita pepo L. **ayote**, **calabaza** (squash). (Standley, 1931:378). Cultivated vine. Eaten cooked as vegetable, in soups, made into bread or sweets. Rind can be prepared as a *guacal* (container), but not as hard as *Crescentia cujete*.

Luffa cylindrica (L.) Roem. **paste** (sponge gourd). (Standley, 1931:380). Large cultivated vine. Native of Old World tropics. Rind removed and interior used as a scrub pad for personal washing.

Momordica charantia L. **caléica** (balsam pear). (Standley, 1931:380). Large or small, slender vine. Wild. Fruit eaten raw. Decoction of leaves and vine said to fortify the blood.

Sechium edule (Jacq.) Sw. **patastillo** (chayante). (Standley, 1931:381). Large vine. Cultivated. Fruit cooked and eaten as vegetable or in stews. Juice made by grinding and pressing the raw fruit is taken as medicine, but informants did not know for what ailment.

Euphorbiaceae

Manihot esculenta Crantz **yuca** (manioc, cassava). (Dickson, 1978:55; Standley, 1931:253–254). Large, bushy or tree-like herb. Cultivated. Native of Brazil. The Chamelecón mestizos recognize three sweet varieties (two white, one yellow) and one bitter variety. Informants described the process for preparing bitter manioc but claimed they don't use it. Starchy tubers of sweet varieties boiled and eaten or made into bread or sweets. Not commercialized. A poultice made of ground leaves used for sunburn.

Fabaceae [=Leguminosae]

Cassia fistula L. **cañafistola** (shower of gold). (Dickson, 1978:26). Small tree. Cultivated. Wood used as firewood and charcoal after tree has died. Seed cases are pounded to remove seeds, which are soaked in water and drunk as a laxative.

Cassia grandis L. **carao** (pink shower). (Dickson, 1978:26; Standley, 1931:218). Tree. Wild. Trunk used for *cayuco* construction, house posts. Wood used for charcoal and firewood. Fruit eaten raw or pounded and placed in sugar water to make juice. Young leaves pressed to get a liquid for curing sores ("lepras").

Enterolobium cyclocarpum (Jacq.) Griseb. **guanacaste** (ear-tree). (Dickson, 1978:40; Standley, 1931). Giant tree. Wild and cultivated. Trunk used for *cayuco* construction, cut at sawmill for planks. Wood use for furniture.

Gliricidia sepium (Jacq.) Steud. **madriado**. (Dickson, 1978:45; Standley, 1931:223–224). Tree. Cultivated. Wood used for firewood, charcoal, houseposts. Planted to create living fence. Flowers eaten: boil, strain, and fry with eggs and lard. Poultice of ground leaves used on allergic rashes; extract from leaves mixed with water and sugar and drunk for same symptoms.

Inga sp. **guama**. (Standley, 1931:211–212). Tree. Wild. Fruit eaten raw. Wood used for firewood, charcoal.

Inga sp. **guava**. (Standley, 1931:211–212). Tree. Wild. Said to be identical to *guama* (*Inga* sp.) except for habitat and color of fruit and bark. Same uses: fruit eaten raw; wood used for firewood, charcoal.

Phaseolus vulgaris L. **frijol** (kidney bean). (Standley, 1931:231). Herbaceous vine. Cultivated. Seeds (beans) eaten in soups or fried.

Pterocarpus belizensis Jacq. **sangre**. Tree. Wild. Wood used for charcoal, firewood; not good for *cayucos* or house-building.

Tamarindus indica L. **tamarindo** (tamarind). (Dickson, 1978:71). Tree. Cultivated. Fruit eaten raw or used for juice for popsicles ("topogigios").

Lauraceae

Nectandra sp. **aguatacillo**. (Standley, 1931:200). Tree. Wild. Trunk used for *cayuco* construction. When young, trunk can be used for house construction. Wood used for furniture. Leftover pieces good for charcoal or firewood, but this tree also cut expressly for those uses, as it is abundant and grows quickly.

Persea americana Mill. **aguacate** (avocado, alligator pear). (Standley, 1931:201). Tree. Cultivated. Fruits eaten raw. Decoction of bark drunk to cure bruises (literally, to cure internal "tumor" after being hit). Decoction of leaves said to increase intelligence, used for "slow" schoolchildren.

Malpighiaceae

Byrsonima crassifolia (L.) DC **nance**. (Dickson, 1978:23; Standley, 1931:243–244). Shrub or tree. Wild. Fruit eaten raw or used with water or milk and sugar to make juice or popsicle. Wood used for firewood, charcoal.

Malvaceae

Hibiscus sabdariffa L. **jamaica** (roselle, Jamaica sorrel). (Standley, 1931:272–273). Many-branched herb. Cultivated. Fruit soaked or boiled in water, sugar added to resulting infusion or decoction, which is drunk fresh or fermented to make “*vino de Jamaica*” (Jamaica wine).

Marantaceae

Maranta arundinaceae L. **yuquilla** (arrowroot). Many-branched herb. Cultivated. Root is used the same way as *yuca* (*Manihot esculenta*): boiled and eaten, processed for starch. *Yuquilla* starch considered better for eating, *yuca* starch better for starching clothes.

Meliaceae

Cedrela mexicana Roem. **cedro** (Spanish or Mexican cedar). (Dickson, 1978:28; Standley, 1931:240). Large tree. Cultivated. Trunk used for *cayuco* construction. Wood used for furniture; planks cut at sawmill for house floors and walls. Not used for charcoal or firewood.

Moraceae

Artocarpus altilis (Parkinson) Fosberg [*A. communis* Forst., *A. incisus* (Thunb.) L. f.] **mazapan** (breadfruit). Large tree; native of East Indies. Cultivated. Trunk used rarely for *cayuco* construction when very large. Fruit cooked and eaten like meat, made into “*atol*” (sweet drink) or bread. Poultice made by soaking a cloth in sap (through cut in bark) applied to pains from sudden movements (“*aire*”).

Musaceae

Musa sp. **platano, banana** (plantain, banana). (Dickson, 1978:56–57; Standley, 1931:139–140). Native of tropical Asia. Cultivated and escaped varieties of *Musa* are found throughout the study area; fruit is eaten raw.

Myrtaceae

Eugenia sp. **uva española**. Small tree. Fruit fermented with water and sugar to make wine.

Eugenia jambos L. **manzana rosa** (rose-apple). (Dickson, 1978:42; Standley, 1931:303). Small to medium tree. Native of southeastern Asia. Cultivated. Fruit eaten raw; said to cause a bad reaction when combined with alcohol.

Eugenia malacensis L. **manzana pera** (Malay apple). (Dickson, 1978:42). Tree. Cultivated. Fruit eaten raw or made into jelly.

Pimenta officinalis Lindl. **pimenta gorda** (allspice). (Dickson, 1978:62; Standley, 1931:304). Small tree. Leaves and fruit used to make decoction; ground fruit added to bread dough.

Psidium guajava L. **guayabo** (common guava). (Dickson, 1978:64; Standley, 1931:305). Shrub or tree. Cultivated and wild. Fruit eaten raw or made into jelly. Wood used for firewood only when tree is dead.

Phytolaccaceae

Petiveria aleaceae L. **ipacina**. (Standley, 1931:188–189). Coarse, erect herb. Wild. Sniffing root said to clear stuffy nose; root boiled in water used to wash head to relieve a cold. Decoction of root also drunk for stomachache and said to cause abortion.

Poaceae [=Gramineae]

Gynerium sagittatum (Aubl.) Beauv. **caña brava** (cane). (Standley, 1931:92). Tall, coarse grass. Wild. Canes lashed to pole frames for house walls, with or without mud daub.

Oryza sativa L. **arroz** (rice). (Standley, 1931:95). Tall, coarse grass. Cultivated in low ground. Seeds are cooked and eaten, made into bread or sweets, or fermented alone or with maize to make *chicha*. Rice is the crop “which yields most” and is the most important crop for home consumption and commercialization.

Panicum maximum Jacq. **zacate guinea** (guinea grass). (Standley, 1931:96–97). Erect perennial grass. Wild (but Standley noted that it was often cultivated, and he considered it the most important pasture grass of Central America). Pasturage, also cut for cattle feed. Can be used for house thatch (stalk with leaves attached), but it takes more time and effort than corozo palm (*Attalea cohune*) and so is mostly used where corozo palms are unavailable. Guinea grass thatch said to last ten years, longer than corozo thatch.

Saccharum officinarum L. **caña** (sugar cane). (Dickson, 1978:86; Standley, 1931:100–101). Cultivated. Native of Old World tropics. Pressed cane juice and locally prepared sugar used in a variety of foods and beverages.

Vetiveria zizanoides (L.) Nash **valeriana**. Cultivated. Native of Old World tropics. Root soaked in water and drunk to calm nervousness or increase intelligence.

Zea mays L. **maíz** (maize, corn). (Standley, 1931:102). Cultivated. Dried seeds ground for tortillas, bread, *atol* (a sweet drink), tamales; can be eaten on the cob as *elote*; toasted seeds ground for *piñol*, a drink similar to chocolate. To make corn *chicha*, seeds are soaked for a day in water, placed in a bag for 2–3 days until they sprout, then fermented with water and sugar. The *chicha* is sometimes distilled to make *guaro*.

Polygonaceae

Coccoloba hirsuta Standl. **uva de monte**. (Standley, 1931:180–181). Large tree. Wild. Fruit rarely eaten. Wood used for firewood, charcoal.

Quinaceae

Quiina schippii Aubl. **quina**. Small tree. Wild. When dead, wood used for firewood, charcoal. Decoction of bark used to wash wounds to prevent infection; decoction also drunk for stomachache or to cause an abortion. Roasted, powdered bark sprinkled on wounds to prevent infection.

Rhamnaceae

Gouania polygama (Jacq.) Urban **bejuco de cerveza** (beer vine). (Standley, 1931:265). Slender shrub. Wild. Vine pounded and boiled in water. Decoction is cooled, sugar added and drunk fresh or fermented. For added flavor and bite, ginger root (*Hedychium coronatum*) is added when boiling the vine.

Rhizophoraceae

Rhizophora mangle L. **mangle colorado** (mangrove). (Standley, 1931:299). Small to medium tree. Wild. Wood used for all parts of house frame; also used as firewood. Bark formerly (to 1954) soaked in water, which was then used to tan leather; bark was sold for this purpose up to that time.

Rubiaceae

Coffea arabica L. **café** (coffee). (Standley, 1931:369). Shrub. Native of tropical Africa. Seeds dried, removed from case, roasted with sugar, and ground to make coffee.

Rutaceae

Citrus aurantiifolia (Christm.) Swingle **limón, lima** (lime). (Dickson, 1978:30; Standley, 1931:236). Tree. Native of Asia. Cultivated. For *limón* variety: fruit juice drunk, has multiple other uses: in cooking, as medicine for nausea, dysentery, rubbed on “worm” or scorpion bites, to clean gold rings. Wood used as firewood only when tree is dead. For *lima* variety: Fruit eaten raw; fruit juice used to relieve tired eyes and for conjunctivitis. Wood used for firewood only when tree is dead.

Citrus paradisi Macf. **toronja** (grapefruit). (Dickson, 1978:31; Standley, 1931:236). Tree. Old World native. Cultivated. Fruit eaten raw; fruit juice drunk fresh or fermented.

Citrus sinensis Osbeck **naranja** (orange). (Dickson, 1978:31; Standley, 1931:236). Tree. Old World native. Cultivated. Fruit eaten raw, fruit juice drunk. Few producing trees in study area, so no longer commercialized.

Salicaceae

Salix chilensis Molina **sauce** (willow). (Dickson, 1978:67; Standley, 1931:162). Tree. Wild. Trunk used for *cayuco* construction. When trunk is under 10 cm diameter, used for house frames. Wood used for firewood, charcoal. Planted to create living fence.

Sapindaceae

Sapindus saponaria L. **palo de hombre**. Tree. Wild. Wood used for firewood. Decoction made with small pieces of the root can be stored, is used for stomachaches or to calm angry children.

Sapotaceae

Calocarpum mammosum (L.) Pierre **sapote**. (Standley, 1931:316). Medium or large tree. Cultivated. Trunk used for *cayuco* construction; leftover pieces used for firewood or charcoal. Fruit eaten raw. Seeds cut in half, interior is grated to extract an oil which is then cooked; this oil is applied to flesh to remove spots from burns and may help cure the burns.

Lucuma sp. **bunkiap**. (Standley, 1931:318). Large tree. Cultivated. Fruit eaten raw.

Solanaceae

Capsicum annuum L. **chile de relleno, chile dulce** (pepper). (Dickson, 1978:25; Standley, 1931:341). Shrub. Cultivated. Used as a condiment in cooking; the *chile de relleno* variety used for stuffed peppers. The leaf of the *chile dulce* variety used in a poultice to treat skin irritation from *chile bravo* (*Capsicum frutescens*).

Capsicum frutescens L. **chile bravo** (hot pepper). (Standley, 1931:341–342). Shrub. Cultivated. Used as a condiment in cooking; pickled in vinegar with onions, garlic and allspice and eaten with meals. Said to be a sexual stimulant.

Sterculiaceae

Guazuma ulmifolia Lam. **cablote**. (Standley, 1931:279–280). Small or medium tree. Wild. Wood used for house frames, cut for firewood, charcoal. Fruit eaten raw, but rarely.

Theobroma cacao L. **cacao**. (Dickson, 1978:72; Standley, 1931:281–282). Small tree. Cultivated. Seeds are toasted and ground. Mixed with toasted corn, the *cacao* powder is used to make hot chocolate; mixed with sugar and water, the powder is cooked to make a “*tableta*” (bar), which can be eaten or saved and used to make hot chocolate. Well-sealed, the *cacao* powder will last up to six months; untoasted, and unground seeds will last as much as a year. *Cacao* seeds are commercialized by the study group.

Verbenaceae

Priva lappulaceae (L.) Pers. **mozote de bomba** (mozotillo). (Standley, 1931:337). Decumbent herb. Wild. Water in which the whole plant including roots has been soaked for several hours is drunk for lower back pain attributed to kidney problems.

Vitidaceae

Vitis tiliaefolia Humb. & Bonpl. **uva de bejuco** (wild grape). (Standley, 1931:267). Large woody vine. Wild. Fruit eaten raw or used with water and sugar to make juice. Standley mentions that it is a water vine, and “if from one of the larger stems a section about a meter long is cut, there issues as rapidly as it can be drunk a stream of clear flavorless liquid.” Among the study group, this liquid is put in the eyes when they sting.

Zingiberaceae

Hedychium coronatum Koenig **gengibre** (ginger lily, butterfly lily). (Dickson, 1978:46). Native of tropical Asia. Cultivated. Root is washed, peeled, pounded, and boiled to make tea. By adding sugar but not boiling, make “*mistela*” (a drink). *Mistela* can be fermented to make wine. The root is also used as a condiment for some sweets. Root is chewed when one’s voice is lost, also as a sexual stimulant.

Unidentified plants (by local name):

Bejuco de ñita. Bignoniaceae. Unidentified woody vine found wild in swamps. Used as lashing in house construction, etc.

Jicaco de monte. Tree. Wild. Wood used for house frames (when 5–10 cm diameter); firewood, charcoal (when > 10 cm diameter).

Frijol de carita (face bean). Fabaceae. Shrub, produces pods of small white beans with a black spot. Cultivated. Beans eaten, commercialized.

Guataúl. Large tree. Wild. Trunk used in *cayuco* construction. Wood used for furniture, house frames; leftover wood from *cayuco* construction used for firewood, charcoal.

Javarea. Tree, produces 7–8 cm long, yellow, four-sectioned fruit. Cultivated. Fruit eaten raw or made into juice. Deadwood used for firewood.

A NEW EXTINCT SPECIES OF *SOLENODON*
(MAMMALIA: INSECTIVORA: SOLENODONTIDAE)
FROM THE LATE QUATERNARY OF CUBA

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ABSTRACT

An extinct species of giant *Solenodon*, *S. arredondoi*, is described on the basis of a partial skull and a small sample of postcranial elements from three Late Quaternary fossil deposits in western Cuba. *S. arredondoi* can be distinguished from all other species of *Solenodon* by its considerably larger size. Cranial features in which *S. arredondoi* differs from the two Hispaniolan species of *Solenodon*, the living *S. paradoxus* and the extinct *S. marcanoi*, include the absence of an os proboscis, relatively broader frontals at the anterior edge of the orbits, more pronounced interorbital constriction, constricted internal narial opening and anterior portion of pterygoid fossa, and much larger posteroventrally expanded pterygoid processes. Dental characters separating *S. arredondoi* from *S. paradoxus* are the greatly enlarged and inflated C¹, lack of accessory cusps on C¹, and presence of a noticeable diastema between P³ and C¹. *S. arredondoi* is closely related to the living Cuban *Solenodon*, *S. cubanus*, but differs from that species in its larger size, as well as the somewhat more constricted interorbital region, narrower internal narial opening, more prominent pterygoid processes, comparatively more inflated C¹, and broader upper molars. The diverse fauna of extinct birds and mammals collected in association with *S. arredondoi* indicates a Late Quaternary age (late Pleistocene or early Holocene) for this species. The giant Cuban *Solenodon* is one of the largest known members of the order Insectivora, living or extinct. It was probably carnivorous, preying on larger invertebrates and a variety of small to medium-sized terrestrial vertebrates.

INTRODUCTION

The existence of a very large extinct species of *Solenodon* from Cuba was first mentioned by Arredondo (1970) based on a femur he collected 16 years earlier from a fossil deposit at Abra de Andrés, in the Sierra de Anafe, La Habana Province, western Cuba. This femur was later figured and described in detail by Morgan et al. (1980). These authors also mentioned the existence of two other large fossil femora of *Solenodon* from western Cuba, one each from Caverna de Pío Domingo, Pinar del Río Province and Cueva Paredones, La Habana Province. Both of these specimens were intermediate in size between the extremely large fossil femur from Abra de Andrés and the living Cuban species, *Solenodon cubanus* Peters. Morgan et al. (1980) did not name a new species because they felt that a single incomplete femur was an inadequate element upon which to describe a new taxon. In early 1991, while examining specimens in the Museo Nacional de Historia Natural in La Habana, Cuba, Oscar Arredondo discovered a partial skull

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Table 1.—Cranial measurements of fossil and Recent *Solenodon* from Cuba. Statistics for the samples of fossil and Recent *S. cubanus* are (in order) mean, standard deviation (± 1 SD), observed range, coefficient of variation, and sample size (N).

Species and locality	Antorbital constriction	Zygomatic breadth	Interorbital constriction	Squamosal breadth	Palatal length	Palatal breadth	Alveolar length of maxillary toothrow
<i>Solenodon arredondoi</i> (type)							
Cueva Paredones							
MNHNC 421/123	19.0	39.0	16.3	35.4	40.7	25.2	28.0
<i>Solenodon cubanus</i> (fossil)							
	17.1 \pm 0.5	34.3 \pm 0.6	15.7 \pm 0.7	31.2	35.7 \pm 1.6	23.7 \pm 0.8	25.2 \pm 0.6
	16.8–17.8	34.0–35.0	15.3–16.2	—	33.9–37.2	22.9–24.3	24.5–26.0
	3.3	1.7	4.1	—	4.4	3.2	2.5
	N = 3	N = 3	N = 2	N = 1	N = 4	N = 3	N = 4
<i>Solenodon cubanus</i> (Recent)							
	15.0 \pm 0.7	32.4 \pm 1.3	15.2 \pm 0.6	30.9 \pm 0.8	34.3 \pm 1.1	21.5 \pm 1.2	23.7 \pm 0.9
	14.3–16.4	30.5–35.2	14.5–16.4	29.6–31.9	31.8–35.7	20.3–23.9	21.8–24.7
	4.8	4.0	4.1	2.6	3.1	5.4	3.7
	N = 14	N = 9	N = 13	N = 12	N = 14	N = 14	N = 14

of a very large *Solenodon* from a fossil deposit in Cueva Paredones. The discovery of this skull permits a thorough description of the previously unnamed giant *Solenodon*. We have also re-examined and measured the three large *Solenodon* femora mentioned in the literature, as well as several additional cranial and postcranial elements that pertain to this new species.

Comparisons and measurements of the *Solenodon* skull from Cueva Paredones reveal that this specimen, like the femur from Abra de Andrés reported by Arredondo (1970) and Morgan et al. (1980), is considerably larger than either of the two extant species of *Solenodon*, *S. cubanus* Peters from Cuba and *S. paradoxus* Brandt from Hispaniola. We present a morphological description and measurements (Tables 1–4) of this new large *Solenodon*, as well as comparisons with the two living and one other extinct species in the genus, *S. marcanoi* Patterson from Hispaniola. The *Solenodon* fossils from western Cuba described here belong to a new species that is not only much larger than any previously described member of the genus, but is also one of the largest known species in the order Insectivora.

METHODS AND ABBREVIATIONS

Explanations of the cranial characters and measurements of *Solenodon* used herein are presented by Ottenwalder (1991). Excellent descriptions and illustrations of the cranial anatomy and dentition of *Solenodon* have been published by McDowell (1958). We follow the standardized dental nomenclature for mammals (e.g., Szalay, 1969). However, the cusp homologies of the upper molars and the molariform P^4 of *Solenodon* are in question. In attempting to demonstrate a close phylogenetic relationship between *Nesophontes* and *Solenodon*, McDowell (1958) interpreted the large central cusp on the P^4 – M^3 of *Solenodon* to be the protocone. He also proposed that the metacone on these teeth was lost and that the paracone was represented by a tiny cusp located on the paracrista anterolabial to the protocone. However, most other authors (Butler, 1937, 1939; Van Valen, 1966, 1967; Hershkovitz, 1971) considered the primary cusp on the upper molariform teeth of *Solenodon* to be the paracone. According to these workers, a metacone is absent and the two cusps on the lingual cingulum are the slightly larger anterolingual protocone and the smaller posterolingual hypocone. We follow the latter dental terminology for *Solenodon* molariform teeth, as it appears to be the most commonly accepted and the least controversial. It should also be noted that mammalian paleontologists have long disagreed on the origin and homology of the central cusp in zalambdodont molars, such as those of *Solenodon*.

There is also some disagreement among previous authors on the dental formula of *Solenodon*, which lacks one tooth in each jaw quadrant compared to the primitive eutherian dentition. The missing tooth is obviously a premolar, but it is unclear whether this is the $P^2/2$ or $P^3/3$. We follow McDowell (1958) who tentatively regarded the missing premolars as the $P^3/3$.

Poduschka and Poduschka (1983) examined the external, cranial, and dental characters used by previous workers to distinguish *Solenodon cubanus* from *S. paradoxus*. In particular, they evaluated the validity of the genus *Atopogale*, established by Cabrera (1925) for *S. cubanus*. It is not our intent to comment extensively on the relationship between *S. cubanus* and *S. paradoxus*, as a thorough systematic review of the genus *Solenodon* has already been undertaken (Ottenwalder, 1991). Our discussion and comparisons are primarily limited to characters that can be observed in the fossil material of the new species of *Solenodon* from Cuba.

The following museums, institutions, and collections possess specimens of Recent and fossil *Solenodon* examined during this study. The abbreviations used in this paper for each of these collections are as follows: Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba, Havana, Cuba (IES/ACC); Jose A. Ottenwalder, private field collections, Santo Domingo, Dominican Republic (JAO); Museum of Comparative Zoology, Harvard University (MCZ); Museo Nacional de Historia Natural de Cuba, Havana, Cuba (MNHNC); Personal collection of Oscar Arredondo, Havana, Cuba (OA); Florida Museum of Natural History, University of Florida (UF); United States National Museum of Natural History, Smithsonian Institution (USNM).

Table 2.—Measurements of upper teeth of fossil and Recent *Solenodon* from Cuba. Statistics for samples of fossil and Recent *S. cubanus* are (in order) mean, standard deviation (± 1 SD), observed range, coefficient of variation, and sample size (N).

Species and locality	Length M ¹ –M ³	Length C ¹	Width C ¹	Length P ¹	Width P ¹	Length P ²
<i>Solenodon arrendondoi</i> (type)						
Cueva Paredones						
MNHNC 421/123	9.7	6.2	4.0	4.0	2.9	5.2
<i>Solenodon cubanus</i> (fossil)	—	4.6 \pm 0.2	3.1 \pm 0.1	3.4 \pm 0.2	2.3 \pm 0.1	3.8 \pm 0.6
	—	4.4–4.8	3.0–3.2	3.2–3.7	2.2–2.4	3.4–4.6
	—	4.7	4.2	6.1	5.1	16.2
	—	N = 3	N = 3	N = 4	N = 4	N = 3
<i>Solenodon cubanus</i> (Recent)	8.6 \pm 0.4	4.5 \pm 0.3	3.0 \pm 0.2	3.1 \pm 0.1	2.4 \pm 0.1	3.8 \pm 0.4
	8.0–9.6	4.1–4.8	2.6–3.2	2.9–3.2	2.4–2.5	3.1–4.2
	5.1	6.1	5.7	3.5	2.1	11.6
	N = 12	N = 12	N = 12	N = 5	N = 5	N = 5

SYSTEMATIC PALEONTOLOGY

Order Insectivora Bowdich, 1821
Suborder Soricomorpha Saban, 1954
Family Solenodontidae Dobson, 1882
Genus *Solenodon* Brandt, 1833
Solenodon arrendondoi, new species
(Fig. 1)

Holotype. — MNHNC 421/123, nearly complete skull lacking only the braincase, with right M¹ and M³ and left C¹, P¹, P², M¹, M². Cueva Paredones, 3 km southwest of Ceiba del Agua, San Antonio de los Baños, La Habana Province, Cuba.

Referred specimens. — Additional fossils from type locality (Cueva Paredones): IES/ACC P-2431/3675, edentulous palatal fragment; IES/ACC uncatalogued, partial braincase, including parietals and occipitals; IES/ACC 278, complete right humerus; MNHNC uncatalogued, right proximal humerus, collected by Manuel Iturralde in April 1991; OA 2943, right femur missing distal end, collected by Oscar Arredondo in September 1959 (Morgan et al., 1980).

USNM 299480, partial left femur from Abra de Andrés, Altura del Esperón, Sierra de Anafe, northeast of Guanajay, La Habana Province, Cuba. Collected by Oscar Arredondo and César García del Pino on 15 March 1959 (Arredondo, 1970; Morgan et al., 1980). As noted by Morgan et al. (1980), this locality was actually in Pinar del Río Province when the specimen was collected, prior to the reorganization of the Cuban provincial boundaries. Under the new geographic subdivision the boundary between the provinces of Habana and Pinar del Río was moved to the west and Guanajay and environs are now in Habana Province.

OA 301E, partial associated skeleton, including: left humerus, right radius, left ulna, right innominate, left femur, right proximal and left distal tibia, and left calcaneum from Caverna de Pío Domingo, Ensenada Pica-Pica, Sierra de Sumidero, Pinar del Río Province, Cuba. Collected by Oscar Arredondo and J. N. Otero, January 1954 (Arredondo, 1955; Morgan et al., 1980).

Diagnosis. — *Solenodon arrendondoi* can be distinguished from all other species in the genus *Solenodon* by its considerably larger size. *S. arrendondoi* differs from the two Hispaniolan species, *S. paradoxus* and *S. marcanoi*, in the absence of an os proboscis, the relatively broader frontals at the anterior edge of the orbits, more pronounced interorbital constriction, constricted internal narial opening and anterior portion of pterygoid fossa, much larger posteroventrally expanded pterygoid processes, and greatly enlarged and inflated C¹. Additional characters separating *S. arrendondoi* from *S. paradoxus* include the presence of a diastema

Table 2.—*Extended.*

Width P ²	Length M ¹	Width M ¹	Length M ²	Width M ²	Length M ³	Width M ³
4.2	4.5	7.5	3.3	7.3	2.2	5.8
3.8 ± 0.8	4.0 ± 0.5	6.5 ± 0.1	3.2	5.8	—	—
3.8–3.9	3.5–4.6	6.3–6.6	—	—	—	—
2.0	11.2	1.9	—	—	—	—
N = 3	N = 4	N = 4	N = 1	N = 1		
3.7 ± 0.3	3.5 ± 0.3	6.7 ± 0.4	2.6 ± 0.3	6.1 ± 0.3	2.0 ± 0.1	4.7 ± 0.3
3.3–3.9	3.2–4.0	6.1–7.4	2.0–3.0	5.7–6.8	1.8–2.3	4.2–5.3
7.1	7.3	6.3	12.5	5.5	6.6	6.6
N = 5	N = 11	N = 11	N = 11	N = 11	N = 11	N = 12

between I³ and C¹ as well as smaller but distinct diastemata between I² and I³ and C¹ and P¹, strong lingual expansion of P², and lack of anterior accessory cusps on C¹, P¹, and P². Besides its larger size, *S. arredondoi* can be distinguished from the other Cuban species *S. cubanus* by its somewhat more constricted interorbital region, narrower internal narial opening, more prominent pterygoid processes, comparatively more inflated C¹, and broader upper molars.

Description and comparisons.—Although the skulls of *Solenodon arredondoi*, *S. cubanus*, *S. marcanoi*, and *S. paradoxus* are generally similar overall, there are numerous morphological features that distinguish the four species. As would be predicted on the basis of geography, *S. arredondoi* is more similar to *S. cubanus* than to the two Hispaniolan species in the genus, *S. paradoxus* and *S. marcanoi*. Only characters that can be observed in the type specimen and referred material of *S. arredondoi* are discussed here. More detailed morphological and mensural comparisons of *S. cubanus*, *S. paradoxus*, and *S. marcanoi* are presented by Ottenwalder (1991).

Table 3.—*Measurements of the humerus of fossil and Recent Solenodon from Cuba. Statistics for the sample of Recent S. cubanus are (in order) mean, standard deviation (± 1 SD), observed range, and coefficient of variation.*

Species and locality	Total length	Proximal breadth	Proximal depth	Minimum shaft width	Distal breadth
<i>Solenodon arredondoi</i>					
Cueva Paredones					
P-278	56.3	13.5	13.0	5.2	20.0
uncatalogued	—	12.6	12.1	4.8	—
<i>Solenodon arredondoi</i>					
Caverna de Pío Domingo					
OA 301E	51.7	12.4	12.3	4.8	18.9
<i>Solenodon cubanus</i> (fossil)					
Cueva Paredones					
IES/ACC P-621	44.3	10.9	9.9	4.2	15.3
<i>Solenodon cubanus</i> (Recent)					
N = 5	43.0 ± 1.3	10.3 ± 0.5	9.7 ± 0.3	3.8 ± 0.1	14.7 ± 0.7
	41.6 ± 44.7	10.0–11.0	9.4–9.9	3.7–4.0	14.2–15.9
	3.02	4.44	2.98	3.00	4.65

Table 4.—Measurements of the femur of fossil and Recent *Solenodon* from Cuba. Statistics for the sample of Recent *S. cubanus* are (in order) mean, standard deviation (± 1 SD), observed range, and coefficient of variation.

Species and locality	Total length	Proximal breadth	Diameter of head	Width at third trochanter	Minimum shaft width	Distal breadth	Distal depth
<i>Solenodon arredondoi</i>							
Abra de Andr�s USNM 299480	66.1	—	—	11.6	7.1	—	14.4
<i>Solenodon arredondoi</i>							
Caverna de P�o Domingo OA 301E	57.8	16.4	8.3	10.5	6.2	14.4	12.7
<i>Solenodon arredondoi</i>							
Cueva Paredones OA 2943	—	16.2	8.0	9.2	6.4	—	—
<i>Solenodon cubanus</i> (fossil)							
Cueva Paredones IES/ACC P-620	48.2	13.3	6.8	6.7	5.1	12.2	9.4
IES/ACC P-2599	—	14.1	6.4	7.3	5.1	—	—
<i>Solenodon cubanus</i> (Recent) N = 5	46.8 \pm 0.9 45.6–47.9 1.87	12.9 \pm 0.5 12.3–13.5 3.81	6.7 \pm 0.3 6.3–7.0 4.65	7.6 \pm 0.7 6.9–8.6 8.80	4.5 \pm 0.2 4.2–4.6 3.85	11.7 \pm 0.7 11.0–12.7 5.82	10.1 (N = 1) — —

The most important characters of the skull and upper dentition common to *S. arredondoi* and *S. cubanus*, and that separate them from *S. paradoxus* and *S. marcanoi*, include the more constricted internal narial opening, expanded pterygoid processes, lack of an os proboscis, and noticeably inflated C¹. In addition to these differences, *S. arredondoi* is characterized by its very large size compared to all other members of the genus (see measurements in tables 1–4). Detailed comparisons of *S. arredondoi* will be made primarily with the two living species of *Solenodon*, *S. cubanus* and *S. paradoxus*.

Until recently, the smallest member of the genus *Solenodon*, *S. marcanoi*, an extinct species from Hispaniola, was known only from the type mandible and several postcranial elements (Patterson, 1962). Patterson originally placed *S. marcanoi* in the monotypic genus *Antilloale*, which was later synonymized with *Solenodon* by Van Valen (1967). Extensive new material of *S. marcanoi* from fossil deposits in southern Haiti, including the first known skulls, has been described elsewhere by Ottenwalder (1991). In addition to the morphological differences mentioned above, *S. arredondoi* is so much larger than *S. marcanoi* that further comparisons are unnecessary.

Perhaps the most prominent differences among the species of *Solenodon* are in the pterygoid region. The opening for the internal nares posterior and dorsal to the palate is much smaller and more compressed in *S. arredondoi* and *S. cubanus* than in *S. paradoxus*. The anterior portion of the pterygoid fossa is also much narrower in the two Cuban species, but is markedly broader posteriorly at the level of the postglenoid processes. In most specimens of *S. paradoxus*, the pterygoid fossa is broadest anteriorly at the posterior edge of the palate and then becomes slightly narrower posteriorly, although in some skulls the pterygoid fossa is essentially parallel-sided. The pterygoid processes are much larger and better developed in *S. arredondoi* and *S. cubanus* than in *S. paradoxus*. The pterygoid processes form a high, thin wall for the pterygoid fossa in the two Cuban species, extending ventrally and posteriorly to about the same level as the postglenoid processes. The reduced pterygoid processes of *S. paradoxus* do not extend nearly as far posteroventrally.

Solenodon arredondoi and *S. cubanus* both possess a more noticeable interorbital (=postorbital) constriction than does *S. paradoxus*. This feature is related not only to the deeper constriction in the two Cuban species, but also to the fact that their frontals are relatively broader and more inflated in the region between the anterior edge of the orbits and the postorbital constriction. Thus, the frontals are distinctly broader at the anterior edge of the orbits in *S. arredondoi* and *S. cubanus* and become narrower posteriorly to the level of the strong interorbital constriction. The frontals are almost parallel-sided in *S. paradoxus* in dorsal aspect and the interorbital constriction is not as prominent.

The os proboscis (=paranasal or prenasal bone) is present in all specimens of *Solenodon paradoxus*, both adult and juvenile, but is absent in *S. cubanus* (Ottenwalder, 1991). In *S. paradoxus*, the anterior edge of the premaxilla dorsal to the I¹ possesses a small concavity or invagination where the os proboscis articulates. There is no articular facet for the os proboscis in *S. cubanus*, and the anterior edge of the premaxilla is squared off and projects somewhat anteriorly. The anterior portion of the premaxilla in the type skull of *S. arredondoi* has the same morphology as does *S. cubanus*, indicating that an os proboscis was absent (Ottenwalder, 1991).

The primary dental differences between *Solenodon arredondoi* and *S. cubanus* on the one hand and *S. paradoxus* on the other are in the canines and premolars. In general, the upper canines and first two upper premolars are noticeably broader and more inflated in the two Cuban species than in the Hispaniolan species. These teeth are more laterally (buccolingually) compressed in *S. paradoxus*. Conversely, the upper molariform teeth (P⁴–M³) of *S. paradoxus* are larger than those of *S. cubanus*. Consequently, *S. cubanus* has a comparatively larger antemolar dentition and smaller molars than does *S. paradoxus*. These same dental relationships hold true for *S. arredondoi*, as the upper canine and premolars of this species are greatly enlarged compared to *S. paradoxus*. The molars are about the same size in the two species even though *S. arredondoi* is considerably larger in all other cranial dimensions (see complete comparisons and measurements in Ottenwalder, 1991).

Another dental difference between the Cuban species and *S. paradoxus* is the presence of a well-developed diastema between I³ and C¹ in *S. arredondoi* and *S. cubanus* and the lack of this diastema in most specimens of *S. paradoxus*. Some skulls of *S. paradoxus* examined do have a slight diastema between these two teeth, but it is never as well developed as in *S. cubanus* or *S. arredondoi*. The two Cuban species of *Solenodon* also have short, but distinct, diastemata between I² and I³ and between C¹ and P¹, both of which are totally absent in *S. paradoxus*.

The most distinctive tooth of *Solenodon arredondoi* and *S. cubanus* is the upper canine. The upper canine of the two Cuban species is much larger than the C¹ of *S. paradoxus*, being strongly inflated, especially in the buccolingual dimension. The C¹ of *S. cubanus* is similar in anteroposterior length to the C¹ of *S. paradoxus*, but is much broader, whereas the C¹ of *S. arredondoi* is far larger than that of any other *Solenodon*. Furthermore, probably because of its inflation, the C¹ of *S. arredondoi* and *S. cubanus* lacks any evidence of accessory cusps. *S. paradoxus* possesses distinct accessory cusps at the base of the crown on both the anterior and posterior edges of the C¹. The presence of the anterior

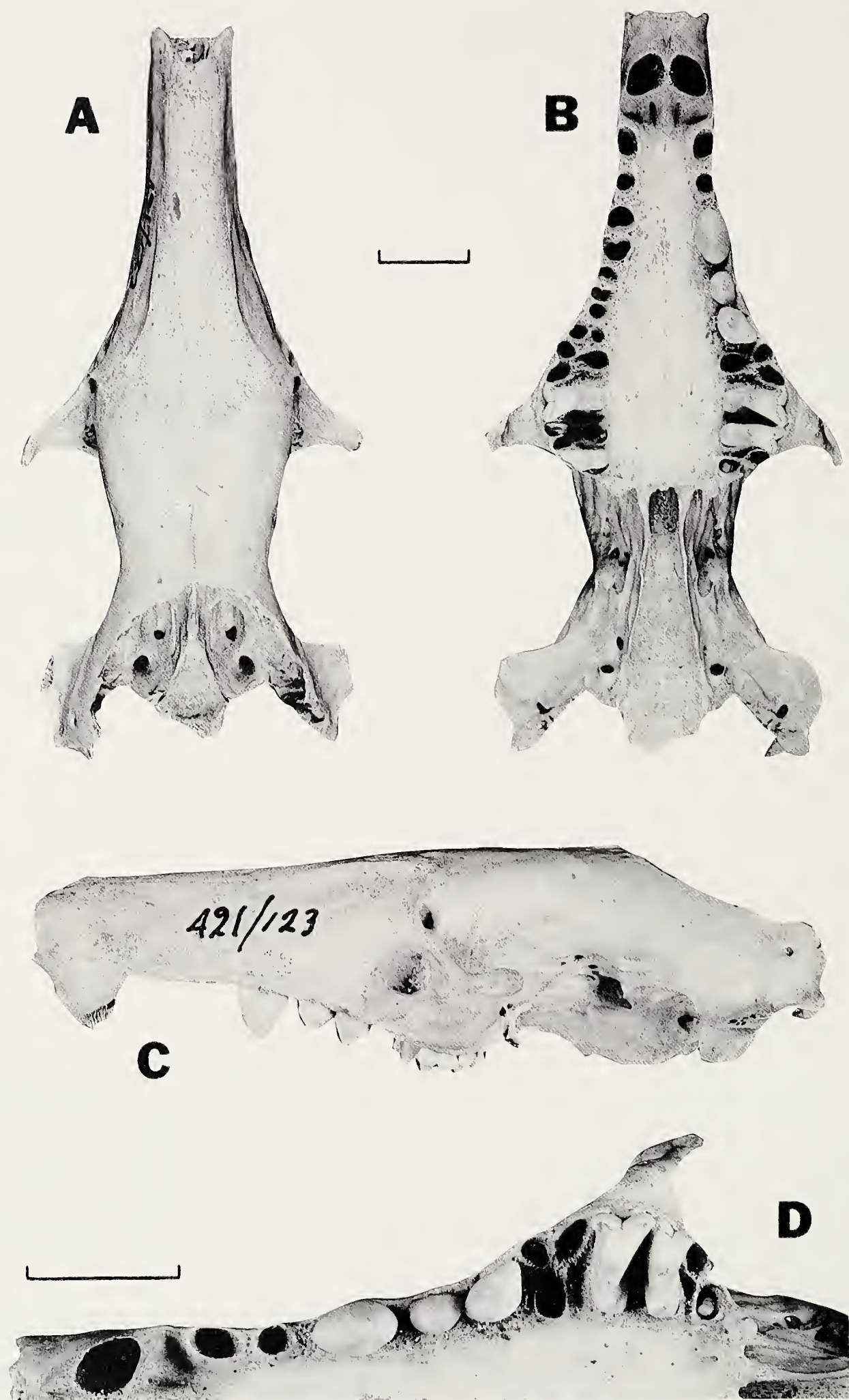


Fig. 1.—Photographs of the holotype skull (MNHNC 421/123) of *Solenodon arredondoi* from Cueva Paredones, La Habana Province, Cuba in dorsal (A), ventral (B, D), and left lateral (C) views. Both scale bars represent 10 mm; the top scale applies to A–C, the bottom scale applies to D.

accessory cusp on the C^1 of *S. paradoxus* has been regarded as one of the most important dental characters distinguishing this species from *S. cubanus* (e.g., Poduschka and Poduschka, 1983). The inflation of the C^1 in *S. arredondoi* and *S. cubanus* and the overall difference in size and shape of this tooth between the two Cuban species of *Solenodon* and *S. paradoxus* seem to be much more diagnostic features than are the accessory cusps.

The type skull of *Solenodon arredondoi* and specimens of *S. cubanus*, both Recent and fossil, also lack anterior accessory cusps on P^1 and P^2 . The C^1 , P^1 , and P^2 all possess anterior accessory cusps in *S. paradoxus*. The P^1 of the two Cuban species is also somewhat inflated in the buccolingual dimension compared to *S. paradoxus*. The P^2 of *S. arredondoi* and *S. cubanus* is relatively large owing to a posterolingual expansion of the tooth, giving it a rounded triangular occlusal outline. The P^2 of *S. paradoxus* generally lacks this lingual expansion, and thus has a narrower more elongated occlusal outline like the C^1 and P^1 . Several specimens of *S. paradoxus* examined had a somewhat triangular-shaped P^2 ; however, this tooth was considerably smaller and less inflated than the P^2 in the two Cuban species. The P^4 of *S. cubanus* also appears to differ in several important features from that of *S. paradoxus*. The P^4 of *S. cubanus* has a more reduced parastyle, a nearly straight labial margin essentially lacking any evidence of an emargination, and a smaller hypocone. The P^4 is not present in the type of *S. arredondoi*. Like the P^4 , the M^1 and M^2 of *S. arredondoi* and *S. cubanus* also have a more reduced hypocone than does *S. paradoxus*.

The most important difference between the two Cuban species of *Solenodon* is obviously the much larger size of *S. arredondoi* compared to *S. cubanus* (tables 1–4). However, there are several other cranial and dental characters that distinguish these two species as well. The internal narial opening in the type skull of *S. arredondoi* is even more constricted than in *S. cubanus*, as is the anterior portion of the pterygoid fossa. The pterygoid processes are also better developed in the larger species, projecting somewhat farther ventrally and posteriorly than in *S. cubanus*. The two Cuban species of *Solenodon* are much more similar to one another in features of the internal nares, pterygoid fossa, and pterygoid processes than either is to *S. paradoxus*. The interorbital constriction in the type skull of *S. arredondoi* is more prominent than in any of the skulls of *S. cubanus* examined. The C^1 is relatively larger and more inflated in *S. arredondoi* than in *S. cubanus*. The M^1 and M^2 in the two Cuban species are similar in anteroposterior length (Table 2); however, these teeth are much broader in *S. arredondoi* giving them a more elongated shape than in *S. cubanus*.

Morgan et al. (1980) described the three femora here referred to *Solenodon arredondoi*. Additional postcranial elements attributed to *S. arredondoi* include a complete and a proximal humerus from Cueva Paredones and a partial skeleton from Caverna de Pío Domingo. All of the available limb bones of *S. arredondoi* are larger than those of the two extant species of *Solenodon* (see measurements of humeri and femora in tables 3 and 4). Although the sample size is quite small, there does appear to be some variation in the size of the postcranial elements referred to *S. arredondoi*. Two of the three femora of *S. arredondoi*, one from Caverna de Pío Domingo (OA 301E) and one from Cueva Paredones (OA 2943), were tentatively identified as *S. cubanus* by Morgan et al. (1980), although they stated that both of these specimens were substantially larger than the single modern femur of *S. cubanus* available to them for study (USNM 49508). Only the extremely large femur from Abra de Andrés (USNM 299480) was considered by these authors to belong to the giant *Solenodon*. We follow Ottenwalder (1991) in referring the two intermediate-sized femora to *S. arredondoi*.

We examined and measured five modern skeletons of *S. cubanus* (tables 3 and 4; see Ottenwalder, 1991, for complete measurements of these specimens), thus providing a better idea of the range of variation present in that species. One complete and one partial fossil femur from Cueva Paredones (Table 4) are within the range of variation of *S. cubanus* in most measurements, whereas the three femora referred to *S. arredondoi* are from 20% (OA 301E and OA 2943) to 30% (USNM 299480) larger than *S. cubanus*. Similarly, the three humeri of *S. arredondoi*, two from Cueva Paredones and one from Caverna de Pío Domingo, average 15–20% larger than *S. cubanus* in most measurements (Table 3).

Certain insectivores, including shrew tenrecs of the genus *Microgale* (see MacPhee, 1987), exhibit a wide range of intraspecific variation in body size. Ottenwalder (1991) presented a detailed statistical analysis of geographic and non-geographic (age, sexual, individual) variation in the two living species of *Solenodon*. Measurements of the available sample of Recent *S. cubanus* (tables 1–4; Ottenwalder, 1991) demonstrate that the type skull and postcranials here referred to *S. arredondoi* are well outside the range of variation in the modern species, and do not represent exceptionally large individuals of *S. cubanus*.

Etymology.—Named in honor of our colleague Oscar Arredondo for his outstanding contributions to the vertebrate paleontology of Cuba. Sr. Arredondo was also the first paleontologist to recognize the existence of this large extinct species of *Solenodon*.

Comparative material examined.—*Solenodon cubanus* (Recent), Cuba: five skulls, two with postcranial skeletons (USNM); five skulls, four with postcranial skeletons (IES/ACC); four skulls (MCZ).

Solenodon cubanus (fossil): IES/ACC P-2325/3645, anterior portion of skull with right P¹–P², M¹; IES/ACC P-621, left humerus; IES/ACC P-620, left femur; IES/ACC P-2599/3678, partial left femur, all from Cueva Paredones, La Habana Province, Cuba (Ottenwalder, 1991).

OA uncatalogued, nearly complete skull with right I¹, C¹, P¹, P², P⁴, M¹, M² and left I¹, C¹, P¹, M². Cueva del Túnel, 3 km SE of La Salud, La Habana Province. Collected by Oscar Arredondo and Noel González, 8 August 1971 (Acevedo et al., 1972; Ottenwalder, 1991).

Solenodon cubanus (archaeological specimens): OA uncatalogued (field #35), anterior portion of skull with right P¹ and left P⁴. Cueva de José Brea, Sierra de Pan de Azúcar, Pinar de Río Province, Cuba. Collected 6–7 November 1949 by Oscar Arredondo (Aguayo, 1950; Arredondo, 1955, 1970; Ottenwalder, 1991).

IES/ACC uncatalogued, anterior portion of skull with right P¹, M¹ and left P¹–P². Los Negros, 25 km south of Baire, Santiago de Cuba Province, Cuba. Collected 19 March 1976 by Ulises Feria Bencosme (Ottenwalder, 1991).

Solenodon marcanoi (fossil): UF 128162, complete skull, Trouing Marassa, La Visite, Haiti; UF 125174, partial skull and partial associated skeleton, Trouing Carfinéyis, Formon, Haiti; UF 128163, 128180, partial skulls, Trouing Jeremie, Formon, Haiti. For a complete list of specimens of *S. marcanoi* see Ottenwalder (1991).

Solenodon paradoxus (Recent), Hispaniola: 65 skulls, most with postcranial skeletons (JAO); 32 skulls, many with complete or partial skeletons (UF).

DISCUSSION

Age and associated vertebrate fauna.—The age of the holotype skull and other fossils of *Solenodon arredondoi* from Cueva Paredones is unclear, as is the age of the fossils of this species from Abra de Andrés and Caverna de Pío Domingo. No radiocarbon dates are available for any of these three localities, and as a consequence faunal associations provide the only clues to the age of the fossils. Arredondo (1976, table 1) provided a list of the associated fossil vertebrates identified from two of the three known localities for *S. arredondoi*, Cueva Paredones (type locality) and Caverna de Pío Domingo. Extinct vertebrates from Cueva Paredones include: the land tortoise *Geochelone cubensis*, the condor *Antillovultur varonai*, the large eagle *Aquila borrasii*, the extinct owls *Pulsatrix arredondoi* and *Tyto noeli*, the giant flightless owl *Ornimegalonyx oteroi*, two species of the small shrew-like insectivore *Nesophontes*, at least five species of small megalonychid ground sloths (*Miocnus antillensis*, *Neocnus gliriformis*, two species of *Mesocnus*, and *Megalocnus rodens*), two species of the echimyid rodent *Boromys*, and as many as five species of capromyid rodents. Numerous specimens of *Solenodon cubanus* were also present in fossil deposits in Cueva Paredones. Manuel Iturralde generously provided us with a sketch map of Cueva Paredones indicating where certain fossils had been found. In April 1991, Iturralde collected a proximal humerus of *S. arredondoi* (MNHNC uncatalogued) about 350 m from the cave entrance and 180 m beyond the Salón del Pozo, a gallery known for the large number of fossils collected there. Except for this humerus, the specific locality within Cueva Paredones where the type skull and remaining fossils of *S. arredondoi* were collected is unknown.

The associated vertebrate fauna from Caverna de Pío Domingo includes *Ornimegalonyx oteroi*, *Nesophontes micrus*, four species of megalonychid sloths (*Miocnus antillensis*, *Neocnus gliriformis*, *Mesocnus torrei*, and *Megalocnus rodens*), two species of *Boromys*, and four species of *Capromys* (Arredondo, 1976). Morgan et al. (1980) discussed the vertebrate fauna associated with the giant *Solenodon* femur from Abra de Andrés, which included four extinct species, three species of megalonychid sloths and the capromyid rodent *Geocapromys columbianus*. Arredondo (1976) also listed *Ornimegalonyx oteroi* from the Sierra de Anafe, Guanajay, presumably from this same site.

The three localities that have produced *Solenodon arredondoi* have similar associated faunas, including *Ornimegalonyx*, as many as five species of megalonychid sloths, and a variety of capromyid and echimyid rodents. These faunas include numerous extinct species, as well as several extinct genera. Although not conclusive, the abundance of extinct taxa would certainly indicate a Late Quaternary age (late Pleistocene or early Holocene) for these three sites. It is difficult to separate late Pleistocene and early Holocene vertebrate faunas from the West Indies (Morgan and Woods, 1986). An abundance of extinct species and lack of evidence of humans characterize most Antillean vertebrate faunas older than about 4500 yBP, the earliest record of Amerindian peoples in the West Indies (Rouse and Allaire, 1978). The reason for the extinction of *S. arredondoi* is unknown, but it is certainly not inconceivable that its disappearance was caused by humans. There is as yet no evidence that the Amerindian inhabitants of Cuba hunted *S. arredondoi*. Habitat destruction and predation by dogs, which were introduced into Cuba by pre-Columbian peoples, are more likely explanations for the extinction of the giant Cuban *Solenodon*.

Distribution.—The three known fossil sites for *Solenodon arredondoi* are all located in western Cuba in La Habana and Pinar del Río Provinces. Cueva Paredones is located near the town of Ceiba del Agua in La Habana Province and is only about 10 km south of the first published site for this species, Abra de Andrés in the Sierra de Anafe just north of the town of Guanajay (Morgan et al., 1980). The third site, Caverna de Pío Domingo, is located near the town of Sumidero in Pinar del Río Province about 120 km southwest of the other two sites. The giant *Solenodon* is very uncommon, having been identified from only three sites out of a total of several hundred Late Quaternary fossil localities throughout Cuba. Based on the fossil record as currently known, *S. arredondoi* may have been restricted to western Cuba.

The Cuban solenodon, *Solenodon cubanus*, still survives in a rather limited area of southeastern Cuba. The historical distribution of *S. cubanus* includes localities in the provinces of Holguín, Granma, Santiago de Cuba, and Guantánamo, all of which were formerly included in Oriente Province (Varona, 1983; Eisenberg and González, 1985; Abreu et al., 1990; Ottenwalder, 1991). *S. cubanus* was rather widely distributed throughout Cuba in pre-Columbian times, particularly at the eastern and western ends of the island. Fossil and archaeological material of *S. cubanus* is known from more than 15 localities in Cuba, including specimens from the provinces of Pinar del Río, La Habana, Matanzas, Camaguey, Holguín, Santiago de Cuba, and Guantánamo (Ottenwalder, 1991). The disappearance of *S. cubanus* from most of its former range in Cuba probably can be attributed to human-related activities, including habitat destruction and predation by introduced cats and dogs.

Paleoecology.—The possible ecological role of the giant Cuban *Solenodon* was discussed by Morgan et al. (1980). The living species of *Solenodon*, *S. cubanus* and *S. paradoxus*, are rather unspecialized predators, feeding on a wide variety of invertebrate and vertebrate prey, including insects, land crabs, land snails, frogs, lizards, snakes, and bird eggs (Varona, 1983; Eisenberg and González, 1985; Ottenwalder, 1985; Abreu et al., 1990; Ottenwalder, 1991). True mammalian carnivores (i.e., members of the order Carnivora) are absent from both Recent and Late Quaternary faunas in the West Indies, disregarding the supposed Cuban fossil canids *Cubacyon transversidens* (Arredondo and Varona, 1974) and *Indocyon caribensis* (Arredondo, 1981), which were almost certainly Amerindian dogs.

The majority of carnivorous niches in Cuba are now filled by nonmammalian predators. The largest native terrestrial vertebrate carnivores in Cuba are the boa *Epicrates angulifer*, several species of raptorial birds, and *Solenodon cubanus*.

Many more large predators occurred in Cuba during the Late Quaternary, including the gigantic flightless owl, *Ornimegalonyx oteroi*, two species of very large barn owls, *Tyto noeli* and *T. riveroi*, the large eagle *Aquila borrasii* (Olson and Hilgartner, 1982, suggested that this species may actually be the same as the gigantic hawk *Titanohierax gloveralleni*), and *Solenodon arredondoi*. There were more species of mammalian prey in Cuba during the Late Quaternary as well. In addition to the four species of the capromyid rodent *Capromys* that still inhabit the Cuban mainland, the Late Quaternary terrestrial mammalian fauna of Cuba was composed of up to five species of small megalonychid ground sloths, several species of the shrew-like *Nesophontes*, two species of primates, two species of small echimyid rodents, and as many as ten species of capromyid rodents. The quoted figures for sloths and capromyid rodents are considerably less than the number of species actually described from Cuba (see lists in Varona, 1974; Morgan and Woods, 1986; Woods, 1989a), but probably more accurately reflect the real species diversity of these groups. However, most of these mammals were larger in body size than the giant *Solenodon*, and thus probably would not have constituted potential prey items. Among the mammals listed, only *Nesophontes* and a few species of rodents, including the two echimyids and several of the capromyids, would have been smaller than *S. arredondoi*.

In most cranial and postcranial measurements, *Solenodon arredondoi* is considerably larger than either of the two extant species of *Solenodon* (tables 1–4; Ottenwalder, 1991), and was thus among the largest known members of the Insectivora, living or extinct. Maximum weights and head–body lengths of the two living species of *Solenodon* (after Ottenwalder, 1991) are 800 g and 360 mm for *S. cubanus* and 1100 g and 390 mm for *S. paradoxus*. By very rough extrapolation from linear dimensions, *S. arredondoi* probably would have weighed from 1500 to 2000 g and would have had a head–body length from 450 to 550 mm. In addition to *S. cubanus* and *S. paradoxus*, the largest living members of the Insectivora are (maximum weights and head–body lengths after Eisenberg, 1981): the tenrec *Tenrec ecaudatus* (2400 g, 390 mm); the moonrat *Echinosorex gymnurus* (1400 g, 350 mm); the European hedgehog *Erinaceus europaeus* (1100 g, 300 mm); and the giant otter shrew *Potamogale velox* (ca. 1000 g, 350 mm).

The largest known insectivore was the enormous erinaceid, *Deinogalerix koenigswaldi*, from the Miocene of Italy, which had a skull 210 mm in length (Freudenthal, 1972). Comparative measurements (in mm) of *Solenodon arredondoi* and *D. koenigswaldi* (measurements in parentheses from Freudenthal, 1972) demonstrate that *Deinogalerix* was nearly twice as large: length from anterior edge of skull to posterior edge of palate, 51 (129); maximum length of humerus, 56 (103); maximum length of femur, 66 (114). The Gargano Peninsula of Italy, where *Deinogalerix* was discovered, was apparently an island in the Miocene. Furthermore, the vertebrate fauna associated with *Deinogalerix* contained several large raptorial birds, but no terrestrial Carnivora (Freudenthal, 1972). It is probably no coincidence that *S. arredondoi* and *D. koenigswaldi* both evolved on islands that were virtually devoid of other terrestrial mammalian predators (Freudenthal, 1972; Morgan et al., 1980).

Remarkable new species of Quaternary vertebrates, such as the giant *Solenodon*, continue to be discovered in the Greater Antilles, despite the fact that these islands have been extensively explored for fossils since early in this century. Perhaps the most spectacular new discovery of a West Indian fossil is the skull of a new genus

and species of extinct howler monkey, *Paralouatta varonai*, recently described from a cave in Pinar del Río Province in western Cuba (Rivero and Arredondo, 1991). Several other new, but so far unnamed, taxa of primates have been reported within the past six years from Jamaica and Hispaniola (Ford and Morgan, 1986; Ford, 1990; MacPhee and Fleagle, 1991). Woods (1989b) described *Rhizoplagiodontia lemkei*, a new genus and species of primitive capromyid rodent with rooted teeth, from several fossil deposits on the southern peninsula of Haiti. Fossils from two separate Quaternary localities in Cuba proved to belong to a bird similar to the genus *Scytalopus*, a member of a family of primitive, weak-flying passerines that are now restricted to southernmost Central America and South America (Olson and Kurochkin, 1987). These and other recent discoveries provide strong evidence that the Caribbean Quaternary vertebrate fauna is still incompletely known. Continued paleontological exploration in the West Indies will surely yield further unexpected finds.

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We would like to express our deepest gratitude to our friend and colleague Oscar Arredondo for permitting us to describe the giant Cuban *Solenodon*. Sr. Arredondo discovered the first fossils of this unique species almost 40 years ago and collected many additional specimens pertaining to it in the ensuing years. For the loan of specimens of *Solenodon*, both Recent and fossil, and for allowing JAO to examine specimens in their collections, we thank Jose Fernandez Milera, Jorge de la Cruz, and Luis de Armas of the Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba; Gilberto Silva Taboada of the Museo Nacional de Historia Natural de Cuba, La Habana, Cuba; Michael D. Carleton, Jeremy Jacobs, Robert Purdy, and Clayton E. Ray of the National Museum of Natural History, Smithsonian Institution; Judy Chupasko, Farish Jenkins, Maria Rutzmoser, and Charles Schaff of the Museum of Comparative Zoology, Harvard University; and especially to Oscar Arredondo for making available the *Solenodon* material from his private collection. Manuel Iturralde hand-carried the type skull of *Solenodon arredondoi* from Cuba so that we could examine and describe it. He also provided us with a sketch map of Cueva Paredones. For helpful comments on the manuscript we thank John F. Eisenberg. During the preparation of this paper JAO was supported by grants to John F. Eisenberg and Charles A. Woods. JAO's trips to Cuba and field work in the Dominican Republic were made possible by grants from Wildlife Conservation International, a division of the New York Zoological Society. This is University of Florida Contribution to Paleobiology Number 408.

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RHYSODINE BEETLES
(INSECTA: COLEOPTERA: CARABIDAE OR RHYSODIDAE):
NEW SPECIES, NEW DATA, AND REVISED KEYS TO *OMOGLYMMIUS*
(SUBGENERA *OMOGLYMMIUS* AND *PYXIGLYMMIUS*)

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ABSTRACT

Three new species of Rhysodidae (Coleoptera: Carabidae or Rhysodidae) are described, *Omoglymmius* (*Omoglymmius*) *sabah* (Borneo), *Omoglymmius* (*O.*) *cupedoides* (New Guinea) and *Omoglymmius* (*Pyxiglymmius*) *multicarinatus* (Sulawesi). Descriptions are given for either males or females of the following four species previously known from only one sex: *Clinidium* (*Mexiclinidium*) *championi* Bell and Bell, *Clinidium* (*C.*) *dubium* Grouvelle, *Rhyzodiastes* (*Temoana*) *propinquus* Bell and Bell, *Omoglymmius* (*O.*) *repetitus* Bell and Bell. Range extensions are given for six species: *Omoglymmius* (*O.*) *sus* Bell and Bell, *Omoglymmius* (*O.*) *ichthyocephalus* (Lea), *Omoglymmius* (*Hemiglymmius*) *javanicus* (Grouvelle), *Clinidium* (*C.*) *rojasi* Chevrolat, *Kaveinga* (*K.*) *abbreviata* (Lea) and *Kaveinga* (*K.*) *histrion* Bell and Bell. The locality for *Omoglymmius* (*Hemiglymmius*) *germaini* (Grouvelle) is confirmed as Java, as previously hypothesized, not Bolivia as designated in the original description. Revised keys to *Omoglymmius* (*Omoglymmius*) and *Omoglymmius* (*Pyxiglymmius*) are provided.

INTRODUCTION

In previous papers (Bell, 1970, 1973, 1975, 1977; Bell and Bell, 1975, 1978, 1979, 1981, 1982, 1985, 1987a, 1987b, 1987c, 1988, 1989, 1991) we have treated the rhysodid beetles of the world. The present paper extends our work by providing descriptions of three new species, descriptions of sexes not previously described for four species, significant range extensions for six species and correction of an erroneous early locality record. A revision of the key to *Omoglymmius* (*Omoglymmius*), which covers 92 species including 14 species described since Bell and Bell (1982), is provided. Also included is a revised key to *Omoglymmius* (*Pyxiglymmius*), incorporating the species described in addition to the ten previously described in Bell and Bell (1982, 1985). Both keys contain geographical distribution information.

Abbreviations used in the text are: BMNH, Natural History Museum, London; CMNH, Carnegie Museum of Natural History, Pittsburgh; CMNO, Canadian Museum of Nature, Ottawa; CNCO, Canadian National Collection, Ottawa; HNHM, Hungarian Natural History Museum, Budapest; LEI, Rijksmuseum voor Natuurlijke Historie, Leiden, Netherlands; SAMA, South Australian Museum, Adelaide; UVM, University of Vermont, Burlington; ZMUC, Zoologisk Museum, Copenhagen. L/GW, ratio of pronotal length divided by its greatest width.

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SYSTEMATICS

*New Species Descriptions****Omoglymmius (Omoglymmius) sabah***, new species
(Fig. 1, 2)

Type specimens.—Holotype female, labelled “Borneo, Sabah, Mt. Kinabalu Nat. Pk., Poring Hot Springs, 500 m., 10.V.87, A. Smetana” (CNCO). Paratypes: one female, labelled “Borneo, Sabah, Mt. Kinabalu N.P. above Poring Hot Springs, 530 m., 9.V.87, A. Smetana” (CNCO); two females, labelled “Borneo, Sabah, Mt. Kinabalu N.P. Por. H.S. area, Langanan Fall, 900 m., 14.V.87, A. Smetana” (CNCO, UVM).

Etymology.—This species is named for the state in which it was first collected.

Diagnosis.—An *Omoglymmius* (*O.*) without postorbital or suborbital tubercles, with a pollinose scarp at base of Stria IV, and the outer pronotal carinae punctate but inner carinae impunctate. Among species with this combination of characters, it is distinguished by having antennal segments V–X punctate, basal punctures in grooves, and many setae along the length of Stria IV.

Description.—Length 5.8–6.5 mm. Antennal segments I–IV very coarsely punctate; segments V–X with coarse basal punctures set in a groove (Fig. 2); head 1.2 times longer than wide; median lobe moderately short, apex narrowly rounded; lateral margin shallowly curved; medial angles obtuse, nearly in contact; posteromedial margin evenly curved into posterolateral margin, posterior margin of temporal lobe thus evenly rounded, occipital angle not distinct; orbital groove fine, fading to line of punctures opposite posterior margin of eye; temporal lobe with 12–15 punctures mainly in posterolateral portion; 1–2 temporal setae; postorbital and suborbital tubercles absent; eye large, round (Fig. 1).

Pronotum moderately elongate, L/GW about 1.40, widest slightly anterior to middle, base and apex narrowed; lateral margins curved, at most scarcely sinuate anterior to hind angle; carinae subequal at middle; medial margin of outer carina slightly sinuate anterior to base; outer carina widest anterior to middle, abruptly, obliquely narrowed to apex; gradually narrowed to base; inner carina widest at middle, gradually narrowed to apex, and nearly to base, but abruptly dilated at extreme base; outer carina with about 14 coarse punctures; inner carina impunctate; pronotum without setae; posternum without distinct precoxal carinae.

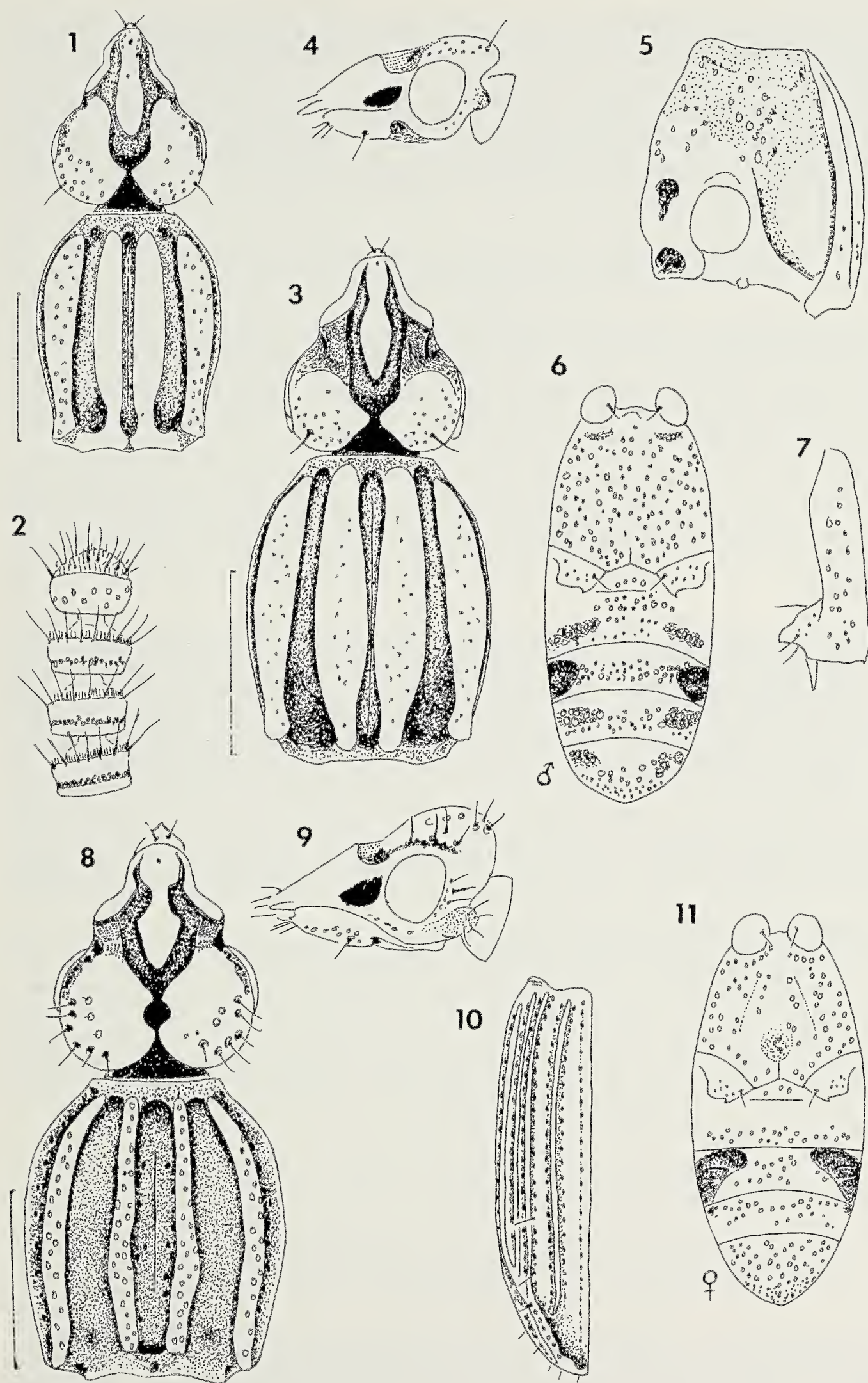
Elytron relatively long, narrow; striae impressed, coarsely punctate; base of Stria IV with longitudinal pollinose scarp; Stria II with 2–3 setae near apex; Stria IV with about seven rather stout setae; apical striole with one seta; extreme apex of Stria VII with 4–5 setae; metasternum with irregularly scattered coarse punctures; punctures of Sterna III–V coarse, numerous, tending to form broad transverse bands; female with shallow lateral pit on Sternum IV, and slight suggestion of one on Sternum V; Sternum VI densely punctate, with one pair of setae; legs coarsely punctate; male unknown.

Distribution.—Known only from the type locality at Mt. Kinabalu.

Remarks.—*Omoglymmius hiekei* Bell and Bell, which was also described from Mt. Kinabalu, differs in that it lacks carinal punctures, temporal punctures, and basal antennal punctures. Grouvelle (1903) described *Rhysodes (Omoglymmius) borneensis* from Sambey River, West Borneo. The holotype has not been located,

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Fig. 1–2.—*Omoglymmius (s. str.) sabah*, new species. Fig. 1.—Head, pronotum, dorsal aspect. Fig. 2.—Antennal Segments VIII–XI. Fig. 3–7.—*Omoglymmius (s. str.) cupedoides*, new species. Fig. 3.—Head, pronotum, dorsal aspect. Fig. 4.—Head, left lateral aspect. Fig. 5.—Prothorax, left ventrolateral aspect. Fig. 6.—Metasternum, abdomen, ventral aspect, male. Fig. 7.—Hind tibia, male. Fig. 8–11.—*Omoglymmius (Pyxiglymmius) multicarinatus*, new species. Fig. 8.—Head, pronotum, dorsal aspect. Fig. 9.—Head, left lateral aspect. Fig. 10.—Left elytron, dorsal aspect. Fig. 11.—Metasternum, abdomen, ventral aspect, female.



but his description stated that the species has punctate inner carinae. Since *O. sabah* has impunctate inner carinae it cannot be conspecific with the Grouvelle species.

One of the paratypes of *O. sabah* has bilateral angular setae. This is highly unusual because the only species of the subtribe of Omoglymmiina to have angular setae is *Xhosores figuratus* (Germar) from South Africa. This singular specimen must be aberrant.

***Omoglymmius (Omoglymmius) cupedoides*, new species**
(Fig. 3–7)

Type specimens. — Holotype male, labelled “Friedrich-Wilh. Hafen, N. Guinea, Biró, 96” (HNHM). Paratype: one female, same data as holotype (UVM).

Etymology. — The name means “resembling the beetle *Cupes*.” This name was selected by O. Adám of the Hungarian Museum who had intended to describe the species. When he learned of our work on the genus he generously allowed us to describe it.

Diagnosis. — An *Omoglymmius* with a postorbital tubercle, a scarp at the base of Stria IV and both inner and outer carinae of pronotum punctate. The lesser width across the postorbital tubercle and the more acute tip on the median lobe separates it from *O. sus*; the narrow, acute median lobe separates it from *O. monteithi*.

Description. — Length 7.0 mm. Antennal segments I–VIII with small basal punctures; segments IX, X more finely punctate; segment XI impunctate; head distinctly longer than wide; median lobe narrowly lance-shaped, frontal space “U” shaped, its margins distinctly curved; medial angles pointed, narrowly separated; posteromedial margins shallowly emarginate; posterolateral margin evenly curved; occipital angle very obtuse; antennal lobe connected to temporal lobe by depressed pollinose ridge; orbital groove absent; temporal lobe with about 20 fine punctures; one temporal seta; postorbital tubercle small, less than 0.25 of length of eye, but visible in dorsal view (Fig. 4); eye large, round.

Pronotum elongate; L/GW about 1.25 (Fig. 3), widest near middle, base slightly narrowed, apex strongly narrowed; lateral margins slightly curved posteriorly, markedly curved anteriorly; margin not sinuate anterior to hind angle; outer carina slightly narrower than inner carina at middle; medial margin of outer carina sinuate, angulate medially; outer carina widest slightly anterior to middle, becoming somewhat narrower toward base; very strongly narrowed to apex; inner carina narrowly truncate at base; outer carina with about 27 fine punctures; inner carina with about 20 fine punctures; prosternum without precoxal carinae (Fig. 5).

Elytron elongate; striae impressed; stria punctures coarse except near apex of elytron; base of Stria IV with longitudinal pollinose scarp; small pollinose spot at base of Stria II; seta at apex of Stria IV present or absent, one seta in subapical striole; 2–3 setae near apex of marginal stria; metasternum entirely coarsely, densely punctate; abdominal Sterna III–V with coarse rather dense punctures except near anterior and posterior margins of each sternum, these punctures confluent near lateral margin; female with deep, narrowly oval, slightly oblique lateral pit on Sternum IV; male with large, deep, round pit on Sternum IV (Fig. 6); male with ventral tooth on profemur, female with obtuse angle in this position; middle calcar narrow, acute, and large; hind calcar triangular, rather deep, tip narrowly rounded, dorsal and ventral margins sinuate (Fig. 7).

Distribution. — Known only from the type locality of Friedrich-Wilhelmshafen, now called Madang, Papua New Guinea.

***Omoglymmius (Pyxiglymmius) multicarinatus*, new species**
(Fig. 8–11)

Type specimen. — Holotype female (unique), labelled “Indonesia: Sulawesi Utara, Dumoga-Bone N.P., April 1985, Plot B, ca. 300 m. lowland forest, flight interception, Trap 3, R. Ent. Soc. Lond, Project Wallace, B.M., 1985-10” (BMNH).

Etymology.—The name refers to the carinate intervals 3, 5, 6, 7 of the elytra.

Diagnosis.—Distinguished by the presence of narrow pronotal carinae, carinate elytra, and setose temporal lobes and the absence of grooves on the lateral metasternum of the female. It differs from all other members of the subgenus in having some elytral intervals carinate. This and the narrow pronotal carinae are suggestive of *Omoglymmius* (*Carinoglymmius*) *hexagonus* (Grouvelle) and *Omoglymmius* (*Carinoglymmius*) *carinatus* (Grouvelle). These two species are known from Borneo, Sumatra, and the Mentawai Islands, and either might be found in Sulawesi. They can be separated from this new species by the evenly curved medial margins of the temporal lobes, the straight tibial spur of the middle leg and the abdominal pits of the female being on Sternum V rather than IV.

Description.—Length 7.8 mm. Antennal segment XI wider than long, obtuse; basal setae and ring setae on segments V–XI; head longer than wide; clypeus impunctate, continuous with median lobe, latter narrow, longer than wide, rhomboidal, tip obtuse; anteromedial margin of temporal lobe oblique; both pairs of medial angles closely approximate; margin between them relatively shallowly emarginate; temporal lobe convex, rounded laterally with about ten punctures in posterolateral fourth, and with orbital groove represented by a row of punctures; approximately six temporal setae; region between temporal and antennal lobes depressed, pollinose; postorbit flat dorsad to postorbital tubercle; both tubercle and postorbit punctate, setose; tubercle relatively small (Fig. 9); gular grooves each with line of four very coarse punctures; most posterior of these on either side of small gular tubercle.

Pronotum L/GW 1.14; subcordate, base distinctly narrowed, apex more strongly so; all grooves much dilated, leaving very narrow, sinuate carinae; carinae and marginal grooves coarsely punctate (Fig. 8).

Elytra elongate, intervals conspicuously unequal, III, V, VI, VII narrow, carinate; I, II, IV scarcely convex; subapical tubercle divided by deeply impressed subapical striole; striae coarsely punctate except near apex where punctures become fine; two setae in apex of Stria IV, one in subapical striole; about five in apex of Stria VII (Fig. 10); female without groove along lateral margin of metasternum; abdominal sterna with coarse, scattered punctures; female with deep, smooth, triangular lateral impressions on Sternum IV, without “brace” or conspicuous striations (Fig. 11); margin of elytral epipleura not angulate opposite sternal pit; profemur of female with slight ventral angle; wings full (tip of wing visible between elytra on type specimen, which was taken in a flight intercept trap), male unknown.

Remarks.—In the key to Rhysodini of Sulawesi and Banggai (Bell and Bell, 1988), this species will trace to the first choice in couplet 3 which should be altered to lead to the new couplet:

- 3.1 Medial margin of temporal lobe emarginate, forming two medial angles
..... *Omoglymmius* (*Pyxiglymmius*) *multicarinatus* new species
- 3.1' Medial margin of temporal lobe not emarginate, one medial angle (*Omoglymmius*, s. str.) 4

Distribution.—Known only from the northern peninsula of Sulawesi (Celebes).

Descriptions of Males and Females Not Characterized Previously
Clinidium (*Mexiclinidium*) *championi* Bell and Bell

Description of female.—6.0 mm, labelled “Guat: Quetzaltenango, 12 km. S.E. Zunil, N.W. face Cerro Zunil, 2700–2760 m., 28.V.1991, R. Anderson, hardwood for. litt. 91–30” (UVM). Very similar to male (Fig. 12, 13) (complete description in Bell and Bell, 1985:62); transverse abdominal sulci represented by lines of isolated punctures interrupted medially; lateral pit of Sternum IV deep, widely flared anteriorly; lateral pit of Sternum V round, small; lateral pit of Sternum III minute; Sternum VI unimpressed, small round lateral pit at anterolateral angle; curved submarginal groove; ventral tooth of profemur absent.

Remarks.—The original description was based on a unique holotype from the Quiché Mountains which did not have precoxal setae. Subsequently we have

studied another specimen with the same locality data and this specimen did have precoxal setae. The female here described also has precoxal setae so the original description should be amended.

Omoglymmius (Omoglymmius) repetitus Bell and Bell

Description of male.—5.8 mm, labelled “N. Sulawesi, Dumoga Bone NP, base camp, alt. m. 211, 13014 1985, J. Huijbregts, RMNH/HH 401, cult. area at light” (LEI). Very similar to female (Fig. 14) (complete description in Bell and Bell, 1982:222); lateral pit of abdominal Sternum IV deep, slightly smaller than in female (Fig. 15); anterior femur with small ventral tooth or tubercle evidently varying in development (distinct, although minute tooth on right femur, but only a well-marked mound-like tubercle on left one in this specimen); middle calcar minute, hind calcar (Fig. 16) moderate in size, obtusely pointed, dorsal margin angled.

Additional collecting data.—All from the Dumoga Bone National Park; one female labelled “Torout, alt. 210 m. 15–16 VIII 1985, J. Huijbregts, secondary growth, river bank, at light” (LEI); one female labelled “27 Feb 1985, lowland forest, Plot C, ca. 400 m., frass under bark of fallen tree” (BMNH).

Rhyzodiastes (Temoana) propinquus Bell and Bell

Description of male.—6.0 mm, labelled “Nicobar, Roepstorff” (ZMUC). Very similar to female (Fig. 17) (complete description in Bell and Bell, 1985:43); metasternum with fine median sulcus, transverse sulci of abdominal sterna broadly interrupted at midline, sulci deeply pilose at medial ends, shallowly pollinose laterally; lateral pit of Sternum IV very deep, that of Sternum V shallow (Fig. 18); posterior one-third of Sternum VI impressed (Fig. 19); ventral tooth of profemur and protibia absent; calcar acute, triangular (Fig. 20).

Remarks.—It is unusual for a male rhyzodid to have a lateral pit on Sternum IV equally deep as that of the female.

Clinidium (Clinidium) dubium Grouvelle

Description of a female.—5.0–6.8 mm (14 specimens) all labelled “Ecuador; Loja, Loja-Saraguro, 2680 m., 18 Nov. 1990, G. Onore, km. 17 of new road Loja to Saraguro, in rotten log in disturbed habitat” (CMNH). Similar to male holotype (Fig. 21) (complete description in Bell and Bell, 1985:115); metasternum with complete narrow pilose median sulcus; pilose median sulcus of Sternum III interrupted at midline, complete on Sterna IV–VI; U-shaped submarginal groove of Sternum VI not connected to transverse sulcus; Sternum IV with large deep lateral pit, that of Sternum V shallow; Sternum VI unimpressed (Fig. 22); ventral tooth of profemur and protibia absent.

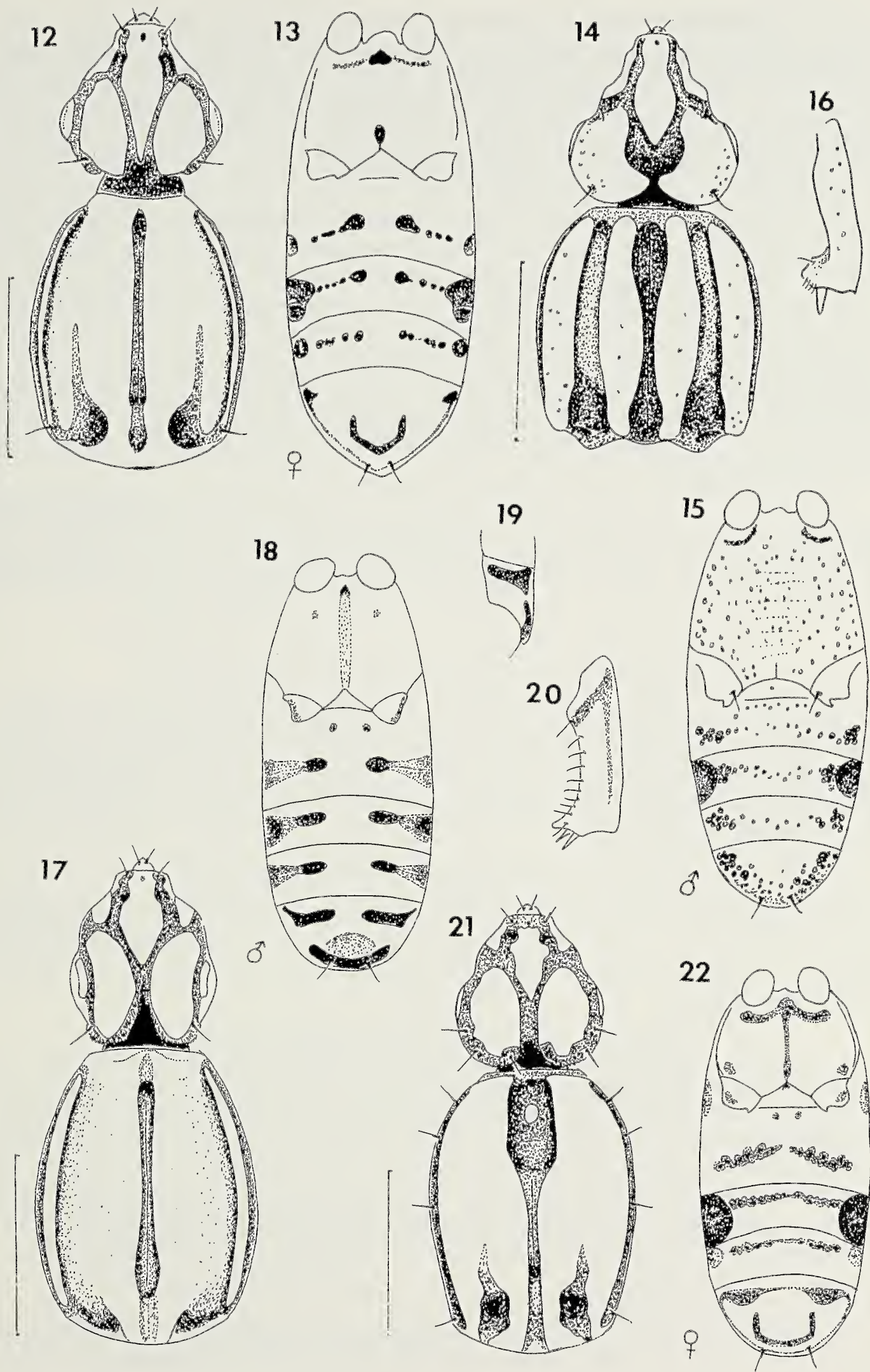
Range Extensions

Omoglymmius (Hemiglymmius) javanicus (Grouvelle, 1903)

All previous collecting sites for *O. javanicus* have been from the western two-thirds of Java, the easternmost point being near Jogjakarta. Two specimens found in the Copenhagen collection, a male (5.6 mm) and a female (6.8 mm) are labelled “Camorta, Nicobar, Roepstorff” (ZMUC), thus extending the range west of Sumatra to the Nicobar Islands.

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Fig. 12–13.—*Clinidium (Mexiclinidium) championi* Bell and Bell. Fig. 12.—Head, pronotum, dorsal aspect. Fig. 13.—Metasternum, abdomen, ventral aspect, female. Fig. 14–16.—*Omoglymmius (s. str.) repetitus* Bell and Bell. Fig. 14.—Head, pronotum, dorsal aspect. Fig. 15.—Metasternum, abdomen, ventral aspect, male. Fig. 16.—Hind tibia, male. Fig. 17–20.—*Rhyzodiastes (Temoana) propinquus* Bell and Bell. Fig. 17.—Head, pronotum, dorsal aspect. Fig. 18.—Metasternum, abdomen, ventral aspect, male. Fig. 19.—Sternum VI, lateral aspect, male. Fig. 20.—Hind tibia, male. Fig. 21–22.—*Clinidium (s. str.) dubium* Grouvelle. Fig. 21.—Head, pronotum, dorsal aspect. Fig. 22.—Metasternum, abdomen, ventral aspect, female.



Omoglymmius (Omoglymmius) ichthyocephalus (Lea, 1904)

This species is described in more detail in Bell and Bell (1991). It was known previously from northern Queensland, Australia, from Cairns north to Cape York. In addition we have seen one male (5.0 mm) and two females (both 7.0 mm) labelled "Mt. Lamington, N.E. Papua, 1300–1500 ft., C. T. McNamara" (SAMA), thus extending the range into Papua New Guinea.

Remarks.—*Omoglymmius ichthyocephalus* was not included in our key to the subgenus (Bell and Bell, 1982) because we were not able to treat the Australian fauna at that time. In our key to the New Guinean species (Bell and Bell, 1982: 192), it traces to *Omoglymmius (O.) oroensis* Bell and Bell. *Omoglymmius ichthyocephalus* differs from the latter species in the following particulars: median lobe (not including clypeus) entirely impunctate; medial angles of temporal lobes closer together; temporal lobes broader; posterolateral margin not bent near temporal seta; orbital groove extended to posterior margin of eye; pronotum less narrowed anteriorly; outer carina narrower and more narrowed at base; inner carina with about ten fine punctures; outer carina with about 35 fine punctures; hind calcar not concave dorsally.

As stated in the original description of *O. oroensis*, several specimens were referred provisionally to that species, although they differed in various minor ways from the holotype. This group of specimens, including *O. ichthyocephalus*, will need further study when more material becomes available. It may be a complex of closely related species, or there may be only one variable species.

Omoglymmius (Omoglymmius) sus Bell and Bell 1982

This species was known previously from New Guinea at Katau, Fly River, Western Province and Morobe Province. One additional specimen has been located in the Copenhagen Museum, a male (8.0 mm) labelled "Bismarck Islands, Lavongai, Banatam, 20 March 1962, Noona Dan Exp. 61-61" [New Hanover Island] (ZMUC). This is an important addition to the inadequately known fauna of the Bismarck Archipelago.

Clinidium (Clinidium) rojasi Chevrolat, 1873

The range of this species is previously given from Falcon State east to Aragua State, Venezuela. A male (5.9 mm) was found in the Copenhagen collection labelled "Guiana, Lansberg" (ZMUC), thus extending the range of this species eastward to Guiana.

Kaveinga (Kaveinga) abbreviata (Lea, 1904)

The subgenus *Kaveinga* is represented by several species in New Britain, the Solomons, New Guinea, and Mindanao but this species has been recorded previously only from various sites in northern Queensland, Australia, from Daintree to Millaa Millaa and Babinda (Bell and Bell, 1991). Recently we have seen two specimens from the Budapest Museum, one male (5.9 mm) labelled "Biró 1898, Sattelberg, Huon Gulf" (HNHM) and one female (6.0 mm) labelled "Biró 1899, Sattelberg, Huon Gulf" (HNHM) which extends the range to New Guinea.

Kaveinga (Kaveinga) histrio Bell and Bell 1979

The species is known from the holotype and two paratypes collected on the east slope of Mt. Apo (Mt. McKinley), 3300 ft Davao Prov., Mindanao, Philip-

pires. One additional female (6.2 mm) specimen has been located labelled “Indonesia: Sulawesi, Utara, nr. Danau Mooat, 1200 m., nr. Kotamobagu, 17 Feb. 1985, rotten log, Roy. Ent. Soc. Lond. Project Wallace, BM 1985-6” (BMNH). This is the first record of this subtribe from the Celebes.

Remarks.—In the key to Sulawesi Rhysodidae (Bell and Bell, 1988:8) this beetle will key to subtribe Omoglymmiina in couplet 1. The key should be altered as follows: The second choice at couplet 1 should lead to couplet 1.1 below;

- 1.1. Median lobe of head elongate extending posteriorly to neck constriction,
widely separating temporal lobes
..... (Rhysodina) *Kaveinga histrio* Bell and Bell
- 1.1' Median lobe not so elongate, not separating temporal lobes
..... (Omoglymmiina) 2

Assignment of the Sulawesi specimen to this species is provisional. The resemblance is very close, but there are few minor differences: the rings of minor setae start on segment six of the antenna (segment five in the Mindanao specimens); the temporal setae are displaced posteriorly, so that the most posterior one is at the margin of the temporal lobe; the pronotum has only one angular seta and is without marginals.

A longer series of specimens from Sulawesi might show that these differences are consistent, or the collection of a male specimen might reveal differences in the calcars or other secondary sexual characters.

Amendment of Locality Data of Previously Described Species

Omoglymmius (Hemiglymmius) germaini (Grouvelle)

This species was described from two specimens in the Paris Museum, both labelled as coming from Cochabamba, Bolivia (Bell and Bell, 1982). We doubted the labels because the species is close to *O. (H.) javanicus* (Grouvelle) from Java, and belongs to a genus not otherwise represented in the neotropical region. Our suspicions were confirmed by a specimen found in the Copenhagen collection labelled “Nongka Djadjar, Øst Java, Aug. 1913, J. Th. Skovgaard” (ZMUC). This locality is at 7.54°S–112.49°E in east Java. The specimen clearly can be distinguished from *O. javanicus* by the outer carina of the pronotum being much more inflated anteriorly.

REVISED KEYS

Key to Adults of Species of Omoglymmius (Omoglymmius)

1. Posterolateral margin of temporal lobe oblique, meeting posteromedial margin at prominent occipital angle; posteromedial margin also oblique, posterior part of temporal lobe nearly rectangular
..... *O. germari* (Ganglbauer)
..... (Europe to western Asia)
- 1'. Posterolateral margin of temporal lobe rounded; occipital angle not prominent; posterolateral margin convex, oblique or emarginate ... 2
- 2(1'). Antennal lobe, postantennal area densely microsculptured, not separated by antennal groove *O. continuus* Bell and Bell
..... (Sula Islands, Indonesia)
- 2'. Antennal lobe glabrous, raised above level of postantennal area, or separated from latter by distinct antennal groove 3

- 3(2'). Inner carina distinctly narrower than outer carina at middle; pronotal grooves coarsely, densely punctate *O. malabaricus* (Arrow)
(southern India)
- 3'. Inner carina equal to or wider than outer carina at middle; pronotal grooves impunctate or sparsely punctate 4
- 4(3'). Temporal lobe nearly circular; frontal space very small, longer than wide; median lobe short, rhomboid; carinae of pronotum only moderately narrowed at base; precoxal carina present 5
- 4'. Temporal lobe reniform or oblique; frontal space larger, in most species wider than long; median lobe either not rhomboid, or, if rhomboid, elongate; inner carina either pointed posteriorly or else constricted just anterior to base, with extreme base widened; precoxal carina present or absent 6
- 5(4). Medial angles of temporal lobes acute, contiguous; Stria IV with 3–5 setae along its length; total length 5.1–5.2 mm .. *O. sakuraii* (Nakane)
(Japan, Viet Nam)
- 5'. Medial angles of temporal lobes obtuse, slightly separated; Stria IV with one or two setae near apex; total length 6.1–7.1 mm
..... *O. laticeps* Bell
(Bhutan)
- 6(4'). Postorbital and suborbital tubercles absent 7
- 6'. Either postorbital or suborbital tubercle present 73
- 7(6). Fourth interval in form of sharp, raised carina *O. bicarinatus* Bell
(Schouten Islands, Indonesia)
- 7'. Fourth interval flat or somewhat elevated, but not carinate 8
- 8(7'). Outer carina at middle equal to or only slightly narrower than inner carina, 0.66 or more of width of inner carina 9
- 8'. Outer carina at middle 0.5 or less of width of inner carina 69
- 9(8). Elytron with short longitudinal scarp at base of Stria IV, pollinose spot medial to it except in *O. summissus* (scarp minute in *O. politus*) 10
- 9'. Elytron without longitudinal scarp at base of Stria IV; pollinose medial spot absent (except in some *O. wallacei*) 51
- 10(9). Either or both pairs of pronotal carinae with six or more punctures (in most species with many more; punctures very fine in *O. vadosus*) 11
- 10'. Pronotal carinae without punctures, or with one or two punctures on inner carina or with one to five on outer carina 49
- 11(10). Inner carina with many punctures 12
- 11'. Inner carina with no, or one to three punctures 33
- 12(11). Two to five temporal setae; posterior margin of temporal lobe bisinuate, forming two projecting lobes in addition to medial angles
..... *O. bituberculatus* Bell and Bell
(Queensland, New South Wales)
- 12'. One temporal seta; posterior margin of temporal lobe evenly curved 13
- 13(12'). Median lobe of head narrow, its margins only slightly curved; outer carina of pronotum broadest at anterior margin, slightly flattened anteriorly; outer carina with lateral margin not sinuate anterior to hind angle *O. summissus* Bell and Bell
(Sumatra)
- 13'. Median lobe relatively broad, its margins more strongly curved; outer carina widest near middle, in many specimens sinuate anterior to hind angle 14

- 14(13'). Orbital groove complete, continuously pollinose to base of temporal lobe 15
- 14'. Pollinosity of orbital groove incomplete, ended posteriorly near posterior margin of eye, or else interrupted there 17
- 15(14). Head relatively broad posteriorly, its lateral margin abruptly rounded near base; latter transverse; anteromedial margin transverse; frontal space broadly U-shaped *O. fringillus* Bell and Bell (in part) (New Guinea)
- 15'. Head not broad posteriorly, lateral margin evenly rounded from eye to base; frontal space more narrow; anteromedial margin oblique 16
- 16(15'). Outer carina markedly narrowed posteriorly, width at base less than 0.5 of greatest width; median lobe narrow, its junction with clypeus distinctly constricted; apex of median lobe obtuse; postantennal area convex, extensively pollinose *O. wittmeri* Bell and Bell (Sula Island, Indonesia)
- 16'. Outer carina scarcely narrowed posteriorly; width at base 0.9 of greatest width; median lobe relatively broad, its junction with clypeus scarcely constricted; apex of median lobe rounded; postantennal area less extensively pollinose *O. gurneyi* Bell and Bell (Solomon Islands)
- 17(14'). Tip of median lobe narrow, subacute; pronotum narrow, lateral margins strongly curved; eye somewhat reduced, with posteroventral margin oblique; antennal segments V–XI impunctate *O. semperi* Bell and Bell (Philippines)
- 17'. Tip of median lobe broadly rounded or obtuse; pronotum quadrate or subquadrate, in most specimens with lateral margins less rounded; eye round, not reduced; antennal segments VII–X in some species with punctures indistinct 18
- 18(17'). Outer antennal segments, including X, with numerous coarse punctures 19
- 18'. Outer antennal segments with punctures sparse, in some species extending only to segment IX 24
- 19(18). Pronotum subquadrate, lateral margins convergent only near apex 20
- 19'. Pronotum with lateral margins curved, convergent from middle to apex 22
- 20(19). Most posterior points on temporal lobes separated from one another by much less than 0.5 width of head 21
- 20'. Most posterior points on temporal lobes separated from one another by more than 0.5 width of head ... *O. fringillus* Bell and Bell (in part) (New Guinea)
- 21(20). Median head lobe punctate *O. oroensis* Bell and Bell (New Guinea)
- 21'. Median head lobe impunctate *O. ichthyocephalus* (Lea) (Australia, New Guinea)
- 22(19'). Medial angle of temporal lobe obtusely pointed; posterior margin slightly sinuate; striae punctures elliptical, fine, sparse *O. viduus* Bell and Bell (Key Islands, Indonesia)
- 22'. Medial angle rounded; posteromedial margin rounded; elytral punctures coarse 23

- 23(22'). Antennal segments V–X as coarsely punctate as segments I–IV; legs, abdominal sterna coarsely punctate *O. puncticornis* Bell and Bell
(New Guinea)
- 23'. Antennal segments V–X more finely punctate than segments I–IV; legs, abdominal sterna more finely punctate *O. tolai* Bell and Bell
(New Britain, Bismarck Island)
- 24(18'). Pronotum elongate, lateral margins only slightly curved; temporal lobe with 30–50 punctures; median lobe obtusely rounded; marginal groove deeper posteriorly *O. scopulinus* Bell and Bell
(Solomon Islands)
- 24'. Pronotum shorter; temporal lobe with 20 or fewer punctures; medial angle produced; posteromedial margin sinuate in most specimens; marginal groove not deeper posteriorly 25
- 25(24'). Median lobe with approximately ten fine punctures
. *O. vicinus* (Grouvelle)
(New Guinea)
- 25'. Median lobe impunctate 26
- 26(25'). Anterior portion of temporal lobe a convex pollinose ridge
. *O. ferrugatus* Bell and Bell
(Celebes)
- 26'. Anterior portion of temporal lobe glabrous, separated from antennal lobe by narrow, pollinose antennal groove 27
- 27(26'). Median lobe narrow, its tip acute 28
- 27'. Median lobe relatively broad, its tip obtuse 29
- 28(27). Pronotum subquadrate, widest, anterior to middle; outer carinae dilated, divergent near base *O. classicus* Bell and Bell
(Admiralty Islands)
- 28'. Pronotum subcircular, markedly narrowed at both base and apex; outer carinae narrow, parallel at bases *O. princeps* Bell and Bell
(Solomon Islands)
- 29(27'). Outer carina narrowed posteriorly, base neither dilated nor divergent 30
- 29'. Outer carina scarcely narrowed posteriorly, base either sinuate medially or else distinctly dilated 31
- 30(29). Pronotum subquadrate, lateral margins nearly parallel; base of pronotum scarcely narrowed *O. lindrothi* Bell and Bell
(Solomon Islands)
- 30'. Pronotum oval, lateral margins strongly curved; base of pronotum distinctly narrowed *O. rusticus* Bell and Bell
(Solomon Islands)
- 31(29'). Medial margin of temporal lobe distinctly angulate opposite tip of median lobe; frontal space more nearly U-shaped
. *O. modicus* Bell and Bell
(Solomon Islands)
- 31'. Medial margin of temporal lobe scarcely angulate opposite tip of median lobe; frontal space more nearly V-shaped 32
- 32(31'). Medial margin of temporal lobe produced, blunt; posteromedial margin emarginate; lateral margins of pronotum markedly curved; lateral pits of abdominal sternum IV shallow in female
. *O. manni* Bell and Bell
(Solomon Islands)

- 32'. Medial angles not produced; posteromedial margin not emarginate; lateral margins of pronotum less curved, subparallel; lateral pits of sternum IV deep, round in female *O. regius* Bell and Bell
(Solomon Islands)
- 33(11'). Lateral abdominal sulci III–V faintly pollinose, distinct punctures absent *O. vadosus* Bell and Bell
(Southern Moluccas, Indonesia)
- 33'. Lateral abdominal sulci III–V with distinct scattered punctures or coalesced punctures 34
- 34(33'). Median lobe very narrow, elongate, margins nearly parallel, tip acute; base of outer carina markedly narrowed .. *O. crassicornis* Bell and Bell
(Philippines)
- 34'. Median lobe moderate in width or broad, margins either parallel or not parallel; base of outer carina less narrowed 35
- 35(34'). Temporal lobe with 5–6 setae *O. aristus* Bell and Bell
(New Guinea)
- 35'. Temporal lobe with 0–1 setae 36
- 36(35'). Antennal segments V–XI punctate 37
- 36'. Antennal segments V–XI with punctures indistinct or absent 39
- 37(36). Antennal punctures in a basal groove; 5–7 setae along Stria IV ...
..... *O. sabah*, new species
(Borneo)
- 37'. Antennal punctures in a slightly scattered ungrooved row; 1–2 setae at apex of Stria IV 38
- 38(37'). Lateral margin of outer carina deeply sinuate anterior to hind angle
..... *O. amplus* Bell and Bell
(Sumatra)
- 38'. Lateral margin scarcely sinuate anterior to hind angle
..... *O. modiglianii* Bell and Bell
(Mentawai Islands, Indonesia)
- 39(36'). Lateral margin of temporal lobe almost straight; anteromedial margin of temporal lobe abruptly bent; frontal space very broad
..... *O. morditus* Bell and Bell
(northern Moluccas)
- 39'. Lateral margin of temporal lobe rounded; anteromedial margin abruptly bent or rounded; frontal space narrower 40
- 40(39'). Head as broad as long or broader than long; frontal space broadly U-shaped 41
- 40'. Head longer than broad; frontal space V- or U-shaped 44
- 41(40). Outer carina slightly narrower than inner carina at middle; marginal groove deep, broad *O. caelatus* Bell and Bell
(Caroline Islands)
- 41'. Outer carina equal in width at middle to inner carina; marginal groove narrow 42
- 42(41'). Antennal groove very narrow; temporal lobes very flat; length 5.0–6.8 mm *O. oceanicus* Bell and Bell
(Caroline Islands)
- 42'. Antennal groove broader; temporal lobes convex; length 6.5–7.2 mm 43
- 43(42'). Pronotum nearly quadrate, scarcely narrowed posteriorly
..... *O. batchianus* (Arrow)
(northern Moluccas)

- 43'. Pronotum distinctly narrowed posteriorly, markedly narrowed anteriorly *O. humeralis* (Grouvelle)
(northern Moluccas)
- 44(40'). Antennal segments V–VIII, and in some specimens also IX, X finely punctate 45
- 44'. Antennal segments V–XI impunctate 47
- 45(44). Inner carina of pronotum constricted just anterior to base; base broadened 46
- 45'. Inner carina not constricted just anterior to base; base truncate ..
..... *O. renutus* Bell and Bell
(Solomon Islands)
- 46(45). Preorbital pit extensively pollinose; median lobe broad
..... *O. trepidus* Bell and Bell
(New Guinea)
- 46'. Preorbital pit with pollinosity restricted; median lobe narrow
..... *O. cavea* Bell and Bell
(New Guinea)
- 47(44'). Temporal lobe punctate over most of its surface; median lobe narrow, tip acute; sides of pronotum nearly parallel
..... *O. philippensis* (Chevrolat)
(Philippines)
- 47'. Punctures of temporal lobe limited to lateral margin; median lobe slightly broader, tip more obtuse; pronotum widest at middle, sides curved 48
- 48(47'). Eye large, round; basal scarp of Stria IV distinct; male with ventral tooth on profemur *O. imugani* Bell and Bell
(Philippines)
- 48'. Eye slightly reduced; basal scarp of Stria IV very small, scarcely more than lateral margin of pollinose spot; male without ventral tooth on profemur *O. politus* Bell and Bell
(Philippines)
- 49(10'). Median lobe broad, margins rounded; abdominal Sterna IV, V with punctures not coalescent *O. opticus* Bell and Bell
(Dammer Island, Lesser Sundas)
- 49'. Median lobe narrow, elongate; Sterna IV, V with punctures coalescent near lateral margins, forming shallow pits 50
- 50(49'). Anterior part of temporal lobe forming narrow pollinose ridge; glabrous area of temporal lobe separated from antennal lobe by nearly length of antennal lobe; temporal setae 0–3 (in most specimens 2); temporal lobe with up to three punctures near lateral margin or none
..... *O. duplex* Bell and Bell
(Philippines)
- 50'. Anterior part of temporal lobe glabrous nearly to antennal lobe, separated from latter only by rather broad antennal groove; one temporal seta; temporal lobe with many punctures
..... *O. bouchardi* Bell and Bell
(Sumatra)
- 51(9'). Inner, outer or both pairs of pronotal carinae punctate 52
- 51'. Pronotal carinae entirely impunctate 64

- 52(51). Inner carina with three or more (in most species many) punctures 53
 52'. Inner carina with one or two punctures or none 56
- 53(52). Head twice as long as wide; median lobe elongate, margins almost parallel *O. nasalis* Bell and Bell
 (southern Moluccas)
- 53'. Head slightly or not at all longer than wide; median lobe lance-shaped, margins not parallel 54
- 54(53'). Outer antennal segments punctate to segment IX; anterior portion of temporal lobe forming pollinose ridge to antennal lobe, broadly separated from glabrous portion of temporal lobe
 *O. wallacei* Bell and Bell
 (Celebes)
- 54'. Outer antennal segments impunctate; anterior portion of temporal lobe glabrous, narrowly separated from antennal lobe by deep pollinose groove 55
- 55(54'). Median lobe constricted at junction with clypeus; tip of median lobe subtruncate; antennal segments IV–IX impunctate; base of outer carina not sloped into basal impression; eye slightly reduced, about 0.33 of length of temporal lobe in profile view ... *O. data* Bell and Bell
 (Philippines)
- 55'. Median lobe not constricted at junction with clypeus; tip of median lobe acute; all antennal segments impunctate; eye not reduced, about 0.5 of length of temporal lobe; base of outer carina sloped gradually into basal impression *O. ephemeris* Bell and Bell
 (New Guinea)
- 56(52'). Intervals II, IV distinctly elevated anteriorly; head elongate anterior to eye; frontal grooves very narrow *O. mycteroides* Bell and Bell
 (Solomon Islands)
- 56'. Intervals II, IV not elevated; head not elongate; frontal grooves moderately broad 57
- 57(56'). Prosternum with precoxal carinae; temporal seta absent
 *O. thoracicus* Bell and Bell
 (Java)
- 57'. Prosternum without precoxal carinae; one temporal seta 58
- 58(57'). Stria IV with five or six setae along its entire length 59
- 58'. Stria IV with one or two setae near apex 62
- 59(58). Outer carina scarcely narrowed at base *O. coelebs* Bell and Bell
 (Philippines)
- 59'. Outer carina strongly narrowed to base; latter bluntly pointed 60
- 60(59'). Median lobe not constricted at junction with clypeus; tip of median lobe rounded; pronotum elongate *O. malaicus* (Arrow)
 (Malay Peninsula)
- 60'. Median lobe constricted at junction with clypeus; tip of median lobe acute; pronotum more nearly quadrate 61
- 61(60'). Bases of outer carinae markedly divergent
 *O. fraudulentus* Bell and Bell
 (Sumatra)
- 61'. Bases of outer carinae scarcely divergent ... *O. nemoralis* Bell and Bell
 (Sarawak)

- 62(58'). Antennal segments V–X with faint basal punctures 63
 62'. Antennal segments V–XI impunctate *O. evasus* Bell and Bell
 (Philippines)
- 63(62). Median lobe of head with punctures; female with round lateral pit
 in Sternum IV (male unknown) *O. brendelli* Bell and Bell
 (Celebes)
- 63'. Median lobe of head without punctures; both sexes with deep di-
 agonal lateral pit in Sternum IV *O. sectatus* Bell and Bell
 (New Guinea)
- 64(51'). Temporal setae absent or one seta 65
 64'. Temporal setae 2–4 68
- 65(64). Median lobe broader, lance-shaped 66
 65'. Median lobe narrow, elongated 67
- 66(65'). Lateral margin of inner carina sloped gradually to groove; temporal
 lobe with few punctures in position of orbital groove
 *O. seriatus* Bell and Bell
 (Celebes)
- 66'. Lateral margin of inner carina deep, sharply defined; temporal lobe
 with 10–12 punctures scattered on lateral half
 *O. gracilicornis* (Grouvelle)
 (New Guinea)
- 67(65'). Abdominal Sterna III–V with coarse punctures, these coalescent near
 lateral margin; Stria IV with one or two setae near apex
 *O. consors* Bell and Bell
 (Sumatra, Borneo)
- 67'. Abdominal Sterna III–V with finer, isolated punctures, not at all
 coalescent laterally; Stria IV with five setae along its length
 *O. hiekei* Bell and Bell
 (Philippines, Borneo)
- 68(64'). Precoxal carinae absent; outer carina as broad as inner one at middle
 *O. quadruplex* Bell and Bell
 (Philippines)
- 68'. Precoxal carina present; outer carina 0.66 as broad as inner carina
 at middle *O. pectoralis* Bell and Bell
 (Java)
- 69(8'). Outer carina of two planes meeting at sharp edge, one vertical, other
 sloped towards paramedian groove; pronotum hexagonal to
 subquadrate; Stria IV with five to seven setae along its length
 *O. tabulatus* Bell and Bell
 (Solomon Islands)
- 69'. Outer carina not formed of two planes; pronotum not hexagonal;
 Stria IV with one or two setae near apex 70
- 70(69'). Head anterior to eye elongate; 1–2 setae on mid section of outer
 carina in most specimens *O. bucculatus* (Arrow)
 (Lesser Sunda Islands, Indonesia)
- 70'. Head anterior to eye not elongate; setae of outer carina absent ... 71
- 71(70'). Punctures present on outer carina *O. patens* Bell and Bell
 (New Guinea)
- 71'. Punctures absent on outer carina 72
- 72(71'). Antennal segments V–X punctured; median lobe parallel-sided, tip

rounded; outer carina 0.3 as wide as inner carina at mid-point; male with ventral profemoral tooth	<i>O. solitarius</i> (Arrow)	
	(Andaman Island)	
72'. Antennal segments V–X impunctate; median lobe lance-shaped, tip obtuse; outer carina 0.5 as wide as inner carina at mid-point; male without ventral profemoral tooth	<i>O. impletus</i> Bell and Bell	
	(Caroline Island)	
73(6'). Suborbital tubercle present		74
73'. Postorbital tubercle present		78
74(73). Outer carina more than 0.6 as wide as inner carina at middle; marginal groove not dilated		75
74'. Outer carina about 0.4 as wide as inner carina at middle; marginal groove dilated	<i>O. pulvinatus</i> (Grouvelle)	
	(New Guinea)	
75(74). Outer carina broadest just anterior to base; base of inner carina strongly narrowed; inner carina impunctate.		
	<i>O. sedlaceki</i> Bell and Bell	
	(New Guinea)	
75'. Outer carina narrowed posteriorly; base of inner carina less narrowed; inner carina punctate		76
76(75'). Median lobe broad, tip subtruncate; pronotum nearly quadrate; metasternal punctures limited to midline and margins		
	<i>O. biroi</i> Bell and Bell	
	(New Guinea)	
76'. Median lobe narrow, tip acute; pronotum not quadrate; metasternum entirely punctate		77
77(76'). Median lobe punctate; outer carina equal to or slightly narrower than inner carina at middle; one temporal seta		
	<i>O. cheesmanae</i> (Arrow)	
	(New Guinea)	
77'. Median lobe impunctate; outer carina distinctly narrower than inner carina at middle; temporal seta absent	<i>O. asetatus</i> Bell and Bell	
	(New Guinea)	
78(73'). Postorbital tubercle visible only in lateral view		79
78'. Postorbital tubercle visible in dorsal view		83
79(78). Lateral margins of pronotum nearly parallel; median lobe broad, rounded; pollinosity of orbital groove extended to posterior margin of eye	<i>O. quadraticollis</i> (Arrow)	
	(Tanimbar, Indonesia)	
79'. Lateral margins more curved; pronotum not subquadrate; median lobe broad to narrow, obtuse to rounded; pollinosity of orbital groove less extensive		80
80(79'). Outer carina narrow, curved, densely punctate		
	<i>O. gressitti</i> Bell and Bell	
	(New Guinea)	
80'. Outer carina not conspicuously narrower than inner carina, sparsely punctate or impunctate		81
81(80'). Inner carina truncate at base; outer carina narrowed to base		
	<i>O. repetitus</i> Bell and Bell	
	(northern Celebes)	

- 81'. Inner carina pointed at base; outer carina dilated at base 82
- 82(81'). Median lobe broad, tip rounded; medial margin of base of outer carina sinuate; pollinose area of orbital groove broad; temporal lobe with scattered, very minute punctures; both pronotal carinae with very minute punctures *O. follis* Bell and Bell
(New Guinea)
- 82'. Median lobe angulate at tip; medial margin of base of outer carina not sinuate; pollinosity of orbital groove limited; temporal lobe with a few minute punctures near lateral margin; pronotal carinae impunctate *O. iridescens* Bell and Bell
(New Guinea)
- 83(78'). Posterior face of temporal lobe with microsculpture in grid pattern; temporal seta marginal 84
- 83'. Posterior face of temporal lobe pilose or scaly; temporal seta not marginal 85
- 84(83). Strial punctures relatively large, round, separated from adjacent punctures by about 0.5 of length of one of them; temporal lobe relatively convex *O. craticulus* Bell and Bell
(New Guinea)
- 84'. Strial punctures small, elliptical, separated by more than length of one of them; temporal lobe strongly flattened
..... *O. planiceps* Bell and Bell
(New Guinea)
- 85(83'). Metasternum entirely punctate 86
- 85'. Metasternum with punctures limited to midline and margins 91
- 86(85). Inner and outer carinae with numerous fine punctures; outer carina narrowed to base; strial punctures round, pilose, coarse 87
- 86'. Outer carina punctate; inner carina impunctate; outer carina dilated at base; strial punctures fine, especially in Striae I-III 89
- 87(86). Width across postorbital tubercle greater than width across temporal lobe *O. sus* Bell and Bell
(New Guinea)
- 87'. Width across postorbital tubercle less than width across temporal lobe 88
- 88(87'). Median lobe rounder, tip obtuse; temporal lobe with posterior medial margin rounded; punctures of temporal lobe finer
..... *O. monteithi* Bell and Bell
(Australia)
- 88'. Median lobe narrow, tip acute; temporal lobe with posterior medial margin slightly emarginate; punctures of temporal lobe coarser ...
..... *O. cupedoides*, new species
(New Guinea)
- 89(86'). Postorbital tubercles very large, divergent; outer carina with many fine punctures; medial angle of temporal lobe rounded 90
- 89'. Postorbital tubercles smaller, scarcely divergent; outer carina with one or two fine punctures; medial angle obtuse *O. lentus* Bell and Bell
(New Guinea)
- 90(89). Outer carina slightly narrower than inner carina at middle; outer carina at anterior 0.33 broader than paramedian groove
..... *O. capito* (Grouvelle)
(New Guinea)

- 90'. Outer carina about 0.5 as wide as inner carina at middle; outer carina at anterior 0.33 narrower than paramedian groove *O. largus* Bell and Bell (New Guinea)
- 91(85'). Postorbital tubercle very large; apex of pronotum less narrowed; strial punctures elliptical, very fine *O. auratus* Bell and Bell (New Guinea)
- 91'. Postorbital tubercle small; pronotum more narrowed anteriorly; strial punctures round, moderately fine 92
- 92(91'). Median lobe broad, tip rounded; width of pronotum at middle subequal to width at base *O. massa* Bell and Bell (New Guinea)
- 92'. Median lobe narrower, tip obtusely rounded; width of pronotum at middle clearly less than width at base ... *O. denticulatus* Bell and Bell (New Guinea)

Key to Adults of Species of *Omoglymmius* (*Pyxiglymmius*)

- 1. Many elytral setae present the length of every stria *O. pilosus* (Grouvelle) (Sumatra, Borneo)
- 1'. Elytral setae absent from some striae. 2
- 2(1'). Elytral intervals III, V, VI, VII narrow, carinate *O. multicarinatus*, new species (Celebes)
- 2'. Elytral intervals not carinate 3
- 3(2'). Median lobe distinctly longer than wide, its apex opposite middle of eye; postorbit in lateral view convex, in form of deep but short, ill-defined postorbital tubercle 4
- 3'. Median lobe transverse, as wide as long, its tip opposite anterior margin of eye; postorbit flat, bounded ventrally by well-defined sub- or postorbital tubercle 6
- 4(3). Medial emargination of temporal lobe relatively shallow, its depth about 0.25 of its length; basal setae present on antennal segments VIII–X *O. lederi* (Lewis) (Caucasus)
- 4'. Medial emargination of temporal lobe deep, its depth 0.5 or more of its length; basal setae present on antennal segments V or VI–X 5
- 5(4'). Temporal lobe broadly rounded posteriorly; postorbital tubercles scarcely visible in dorsal view; anteromedial margin of temporal lobe strongly curved *O. subcaviceps* (Grouvelle) (Viet Nam)
- 5'. Temporal lobe with distinct occipital angle, margin markedly oblique between occipital angle and eye; postorbital tubercles prominent in dorsal view; anteromedial margin of temporal lobe oblique *O. crassiusculus* (Lewis) (Japan)
- 6(3'). Five to six setae present on length of Stria II, IV *O. krikkeni* Bell and Bell (Sumatra)
- 6'. Setae absent from Stria II, 0–2 setae present near apex of Stria IV .. 7
- 7(6'). Outer carina of pronotum distinctly narrower than paramedian groove;

- outer carina nearly straight, of even width *O. armatus* (Arrow)
(Andaman and Nicobar Islands)
- 7'. Outer carina wider than paramedian groove, widest near middle,
tapered both anteriorly and posteriorly 8
- 8(7'). Postorbital tubercles large, prominent in dorsal view; paramedian
grooves relatively shallow 9
- 8'. Postorbital tubercles relatively small, not prominent in dorsal view;
paramedian grooves deep, more sharply defined 10
- 9(8). Elytral intervals flat; intervals, pronotal carinae, temporal lobes
strongly microsculptured in female; lateral pit of Sternum IV in female
longitudinally striate, brace weakly developed . . . *O. opacus* Bell and Bell
(Sumatra)
- 9'. Elytral intervals convex; intervals, pronotal carinae, temporal lobes
shining without microsculpture; in female, lateral pit of Sternum IV
not striate, brace strongly developed *O. hesperus* Bell and Bell
(Mentawai)
- 10(8'). Apex of antennal segment XI with short, stubby stylet; temporal lobes
with 20 or more punctures *O. cristatus* Bell and Bell
(Philippines)
- 10'. Apex of antennal segments XI without stylet; temporal lobe with 1–
12 punctures *O. strabus* (Newman)
(Borneo, Java, Sumatra, and Malay Peninsula)

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REVIEWS

TREES OF NIGERIA. R. W. J. Keay. 1989. Clarendon Press, Oxford. 488 pp., 165 figs. ISBN 0-19-854560-6. \$99.00.

The gap between fully-documented major floras and identification manuals intended for use by non-specialists is especially great in tropical areas of the world. The few such guides which exist, such as the *Trees and Shrubs of Mexico* (Standley, 1920-1926) or the works on the trees of Puerto Rico (Little and Wadsworth, 1964; Little et al., 1974) are well-known and essential volumes in the libraries of both biologists and amateurs interested in the natural history and ecology of those areas. For tropical Africa, there are even fewer such works, especially in English, and one of the most useful is *Nigerian Trees* (Keay et al., 1960-1964), now out of print.

Trees of Nigeria is a revised and abbreviated version of *Nigerian Trees* by the senior author of the original. Although condensed into one volume, the number of families, genera, and taxa represented in this recent publication have all increased. This is due both to newly recorded indigenous species as well as to the inclusion of more exotic trees. Nearly 1000 species of trees in 86 families are included in *Trees of Nigeria*.

This book purports to contain an exhaustive coverage for all native savanna trees which normally reach a height of at least 5 m and native forest trees normally 8 m or more tall. Thus, many small understory trees are not included. This lack is especially noticeable in families such as Rubiaceae and Piperaceae where familiar common understory genera (e.g., *Psychotria* and *Piper*) are completely missing from *Trees of Nigeria*. Similarly, plants which might be considered to be either small trees or shrubs, such as the common coastal species *Conocarpus erectus*, are also missing.

Although many species descriptions are condensed or even eliminated, especially for very rare taxa or for trees considered to be so well known as not to need one (for example, coconut palm), most widespread and common species are fully described. In fact, most species have two sections—the first consisting of brief diagnostic notes which often distinguish the tree from closely related species and a second more detailed morphological account. As one of the main objectives of *Trees of Nigeria* was to produce a single volume which would be useful as a field guide to non-specialist botanists, foresters, ecologists, zoologists, and others, only the more common technical terms are used in the species accounts and a five-page illustrated glossary is included.

In addition to the descriptions, general geographical distribution and brief habitat comments are included for each species. Although authors are given for all subfamily taxa, the citation for publication of the name is not included unless the name does not appear in the *Flora of West Tropical Africa* (FWTA) (Hutchinson and Dalziel, 1953-1972). Whenever possible, a page reference to FWTA is included for each species, and when not possible, references are given to other African floras or revisionary works. Synonyms are not included unless the synonym was the accepted name in FWTA or *Nigerian Trees*.

Although there are separate keys to families, genera, and species, the couplets

of these keys are numbered, but not indented, apparently to save space. This creates problems in using them efficiently and accurately, especially with the larger keys for botanists accustomed to an indented style. The family key focuses on easily observable characters such as leaves and sap, and then on fruits, which the author believes to be more available than flowers. While such features as sap may be useful in field identification, these characters are more limited when applied to herbarium specimens, which often do not include notes on these characters!

The 165 figures in the book illustrate 55 of the 86 families and 161 of the 417 genera included. Most illustrations are full-page black-and-white line drawings, many with details of fruits or flowers, and are generally adequate aids for identification purposes. They are reproduced mostly from *Nigerian Trees* or from *FWTA*. This book is weak on illustrations, a major deficiency for a field volume of this type. At minimum, every family should be represented by at least one illustration. The size of the present illustrations could have been reduced without decreasing their usefulness and other drawings added without increasing the total number of pages.

The size of the original *Nigerian Trees* was much reduced by the complete omission of specimen citations. Although such citations are useful, especially to botanists working in herbaria which may have the originals or duplicates of the cited collections, the convenience of a one-volume work which can be easily carried in the field outweighs the lack of such citations. An argument could be made for the listing of at least one or two specimens, especially for rare or non-illustrated taxa, to enable those with access to specimens to more easily verify determinations.

Perhaps of greatest use in quick field identification are the listings of names in local languages. There are separate vocabularies of vernacular names for Edo, Hausa, Igbo, and Yoruba plus one list which includes names in 27 other languages as well as Arabic. However, a combined alphabetical index of all vernacular names would be of greater utility, especially if the language of the common name is not known. Although the foreword warns against the use of vernacular names alone, even these separate lists, when used in conjunction with the descriptions and illustrations, will certainly speed the process of identification.

With caution, the work can be used to a limited extent for other west African countries. The keys allowed identification of specimens from Cameroon of many common taxa, such as *Glyphaea brevis* and *Musanga cecropioides*, but failed to arrive at satisfactory results for other collections. For example, although a specimen of *Morinda geminata* keyed readily to the genus, the only species in *Trees of Nigeria* is *M. lucida*.

The book is well-bound, printed on high-quality paper, and has a plastic cover which should protect it during field use. Although obviously intended more for field identifications than for use in the herbarium, the high price of this work might prevent some from taking it along for fear of loss or damage. Although *Trees of Nigeria* suffers from many of the problems of limited coverage inherent in this type of work, it ably fills the need for such a manual in tropical Africa.

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- 5) Unpublished dissertation:

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BAT (MAMMALIA: CHIROPTERA) RECORDS, EARLY COLLECTORS, AND FAUNAL LISTS FOR NORTHERN CENTRAL AMERICA

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ABSTRACT

Forty-one species of bats from northern Central America are discussed in relation to their known distribution, some because of re-examination of historic or recent records relating to them. These species include new records for Guatemala (2), Belize (1), Honduras (11), and Nicaragua (2); range extensions in the Neotropics for six species are based on specimens from Belize (1), Honduras (4), and Nicaragua (1); and one record is deleted for Nicaragua. Additional noteworthy records are reported for 15 taxa. Previous identification, locality record, or status of certain museum specimens representing published records were re-examined, and corrections and additional information are reported for 17 species. Brief historical sketches acknowledge a number of resident and visiting naturalists who were important early contributors to our knowledge of the bat fauna of northern Central America. A checklist of 119 species from this region is documented and discussed.

RESUMEN

En este estudio se discuten cuarenta y una especies de murciélagos conocidas en el norte de Centro América en relación a su distribución, algunas a causa del nuevo examen de los registros históricos o recientes que les concierne. Estas especies se incluyen registros nuevos para Guatemala (2), Belice (1), Honduras (11), y Nicaragua (2); las expansiones del alcance en los neotrópicos para seis especies se basan en especímenes de Belice (1), Honduras (4), and Nicaragua (1); y un registro está borrado de Nicaragua. Notables registros adicionales han sido documentados por 15 especies. La identificación anterior, la localidad de registro, o el estado de ciertos especímenes del museo en representación registros publicados que fueron reexaminados, y correcciones e información adicional se han apartado para 17 especies. Recuentos históricos breves reconocen a ciertos naturalistas residentes o extranjeros que fueron importantes contribuidores pioneros a nuestro conocimiento de la fauna de los murciélagos en el norte de Centro América. Una lista de 119 especies que habitan esta región está documentada y discutida.

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INTRODUCTION

The northern Central American countries of Guatemala, Belize, El Salvador, Honduras, and Nicaragua encompass a diverse physiography spanning the isthmus from a dry, narrow Pacific coastal plain across a mosaic of arid to moist internal montane valleys to humid Caribbean lowlands. The topography is punctuated by uplifted landmasses and volcanic formations that extend southeastward from Chiapas to Nicaragua. The region between the Isthmus of Tehuantepec and the Nicaraguan depression has been referred to as Nuclear Central America (Schuchert, 1935). This Central American core region is of biogeographical interest because it lies between North and South America. It has a bat fauna comprised of Nearctic, Neotropical, and pan-American elements, in addition to its endemic taxa.

Efforts to document the bat fauna of the region have been especially numerous during the last 25 years. Publications on the bats of Guatemala, Belize, El Salvador, Honduras, and Nicaragua include those of Davis and Carter (1962*a*), Silva-Taboada and Koopman (1964), Starrett and de la Torre (1964), Davis et al. (1964), Jones (1964*a*), Peterson (1965), Jones (1966), Carter et al. (1966), Villa-R. (1966), Disney (1968), Rick (1968), LaVal (1969), Valdez and LaVal (1971), Jones et al. (1971), Harrison and Pendleton (1973, 1974), Jones and Bleier (1974), Kirkpatrick et al. (1975), Baker and Jones (1975), Taibel (1977), Cartwright and Kirkpatrick (1977), Quinones et al. (1978), Greenbaum and Jones (1978), Pendergast (1979), Dolan and Carter (1979), Dickerman et al. (1981), McCarthy (1982), McCarthy and Bitar (1983), Ruiz (1983), Benshoof et al. (1984), Hellebuyck et al. (1985), Hill (1985), Hoffmann et al. (1987), McCarthy and Blake (1987), McCarthy (1987), Owen et al. (1990), Marshall et al. (1991), Lee and Bradley (1992), and McCarthy et al. (in press). Jones and Owen (1986), McCarthy (1987), and Owen et al. (1991) provided checklists for Nicaragua, Belize, and El Salvador, respectively. Systematic and cytogenetic investigations on the bats of these countries have resulted in analysis of a number of genera and description of additional taxa: Davis and Carter (1964), Davis (1965, 1968, 1969, 1970*a*, 1970*b*, 1973, 1976, 1984), Pine et al. (1971), Baker and McDaniel (1972), Smith (1972), Baker et al. (1972), Pine (1972), LaVal (1973*a*, 1973*b*), Wilson (1976), Eger (1977), Bickham and Baker (1977), Davis and Carter (1978), Freeman (1981), Honeycutt et al. (1981), Koop and Baker (1983), Baker et al. (1985), Bickham (1987), Arita and Humphrey (1988), and Dolan (1989).

In preparation of a comprehensive review of the bat fauna of the Central American core region, specimens in numerous museums in North and Central America and Europe have been examined to verify identifications and data. Country records and range extensions for 18 species are herein reported in Guatemala, Belize, Honduras, and Nicaragua. We also correct identifications and errors in information associated with certain historic or recent records. Information pertaining to early collectors was gathered, and we present brief biographical sketches of these men and their activities.

ABBREVIATIONS AND MEASUREMENTS

The following institutions house specimens referenced in this report. We also list (in parentheses) names of collectors responsible for the specimens. AMNH—American Museum of Natural History, New York (Guatemala: A. W. Anthony, T. Larson, T. J. McCarthy. Honduras: T. J. McCarthy, C. F. Underwood. Nicaragua: W. B. Richardson); ANSP—Academy of Natural Sciences of Philadelphia (Honduras: J. T. Emlen, C. B. Worth); BMNH—British Museum (Natural History), London (Guatemala: O. Salvin. Belize: R. H. L. Disney, A. M. Hutson. Honduras: B. H. Gaskell. Nicaragua: E. Belcher, W. B. Richardson); CM—The Carnegie Museum of Natural History, Pittsburgh (Guatemala:

N. A. Bitar. Belize: C. T. Agostini, E. R. Blake, T. J. McCarthy, M. Reed. El Salvador: J. G. Owens. Honduras: G. A. Cruz, E. Espinosa); FLMNH—Florida Museum of Natural History, University of Florida, Gainesville (Guatemala: H. Popenoe. Honduras: G. W. Van Hynning); FMNH—Field Museum of Natural History, Chicago (Guatemala: L. de la Torre. Belize: T. J. McCarthy. Honduras: P. O. McGrew); KU—Museum of Natural History, University of Kansas, Lawrence (Nicaragua: J. K. Jones, Jr.); MNHNG—Museo Nacional de Historia Natural Jorge A. Ibarra, Guatemala (Guatemala: unknown); MSB—Museum of Southwestern Biology, University of New Mexico, Albuquerque (Belize: J. Serach); MVZ—Museum of Vertebrate Zoology, University of California, Berkeley (Guatemala: E. J. Koford); SMNS—Staatliches Museum für Naturkunde, Stuttgart (Guatemala: F. C. Sarg); TCWC—Texas Cooperative Wildlife Collections, Texas A & M University, College Station (Guatemala: D. C. Carter, D. A. Christopher, W. B. Davis. Honduras: R. D. Bradley, D. C. Carter, J. Ensink, G. H. Jarrell, R. K. LaVal, T. E. Lee, R. D. Lord, D. L. Mankins, J. V. Mankins, T. C. Maxwell, J. R. Meyer, R. Valdez, J. T. Webb. Nicaragua: D. C. Carter, I. F. Greenbaum); TTU—The Museum, Texas Tech University, Lubbock (Guatemala: P. G. Dolan. Honduras: R. J. Baker, W. J. Bleier, I. F. Greenbaum, V. R. McDaniel, C. S. Rouk, T. L. Yates); UCLA—Department of Biology, University of California, Los Angeles (Nicaragua: O. M. Buchanan); UMMZ—Museum of Zoology, University of Michigan, Ann Arbor (Belize: O. Murie); UNAH—Museo de la Fauna, Universidad Nacional Autónoma de Honduras, Tegucigalpa (Honduras: A. Ayala, S. Flores, B. Myton, R. Sánchez, S. Thorn, M. Villeda); USAC—Colecciones Zoológicas de Referencia, Universidad de San Carlos, Guatemala (Guatemala: J. L. Darling); USNM—National Museum of Natural History, Washington (Guatemala: R. G. McLean, S. R. Ubico. Belize: E. L. Tyson. Honduras: H. W. Perry, C. H. Townsend, G. W. Van Hynning); UTACV—Collection of Vertebrates, University of Texas, Arlington (Guatemala: J. A. Campbell, P. A. Davis); WNMU—Biology Collection, Western New Mexico University, Silver City (Belize: B. J. Hayward, P. Savoie, J. Serach).

Measurements are given for species not well represented by Central American collections in museums. Cranial and forearm measurements are in millimeters; greatest length of skull, breadth across molars, and length of maxillary toothrow are alveolar; condylobasal length is from the occipital condyles to the tip of the premaxillary; the right forearm was measured when possible. All measurements were recorded to the nearest 0.05 mm; weights are in grams. Elevations near sea level are abbreviated s.l.

SPECIES ACCOUNTS

The arrangement of species accounts and nomenclature follow Jones et al. (1988), unless otherwise stated.

Family Emballonuridae

Saccopteryx leptura (Schreber, 1774)

This small sac-winged bat occupies the Middle American lowlands (near sea level to 450 m) along the Pacific versant north to Chiapas and the Atlantic versant to southern Belize (McCarthy, 1987). Greenbaum and Jones (1978) reported *S. leptura* from the Pacific lowlands of Departamento de Valle, Honduras. Additional specimens (TCWC, TTU) document similar localities in Valle (11.8 km SSW San Lorenzo) and Choluteca (17.8 km S Choluteca).

Two specimens in fluid (USNM 16134) from northern Honduras were obtained by C. H. Townsend in the vicinity of Trujillo, Colón, in September 1887. One is identifiable as *Rhynchonycteris naso*, but the other represents *S. leptura*. Townsend's mammal collection was reported by True (1888), but the *R. naso* from Trujillo was the only bat listed. The specimen of *S. leptura* is the sole record for the Caribbean lowlands of Honduras.

Cormura brevirostris (Wagner, 1843)

The northernmost records of *Cormura* are from Peña Blanca and Prinzapolka on the Caribbean slope of northern Nicaragua (J. A. Allen, 1910; Sanborn, 1937). W. B. Richardson collected two specimens (AMNH) of *C. brevirostris* in the area of the mountain Peña Blanca during May 1909. Allen (1910) first reported these

as *Peropteryx canina*. Allen (1910) clearly referred to Peña Blanca as a high point in the otherwise lowland Atlantic slope of Matagalpa in northern Nicaragua. This locality was erroneously plotted by Hall (1981) in the Pacific corridor of southern Rivas. Possibly he confused the name with that of the Costa Rican town of Peñas Blancas, which straddles the Nicaraguan border. This locality also is not to be mistaken for the Peña Blanca discussed by Belt (1888).

Earlier, in 1896, Richardson collected a male specimen (BMNH) in the vicinity of San Emilio, at the southern end of Lago de Nicaragua. See discussion of this locality in the account of *Ectophylla alba*. We know of no recent records of *C. brevirostris* from Nicaragua.

Balantiopteryx plicata Peters, 1867

HONDURAS. Choluteca: Agua Caliente, 9.6 km NW Choluteca, 8 m, 7 males, 3 females (TCWC); 11.2 km SE San Lorenzo, 8 m, 1 female (TCWC). Francisco Morazán: Campamento El Rosario, Parque Nacional La Tigra, 1 male (UNAH). Lempira: Gracias, 820 m, 3 females (FMNH); Quebrada del Amatillo, La Virtud, 4? (UNAH). Santa Bárbara: 5 km NE Llama, 120 m, 14 males, 15 females (TCWC); Macholua, 1 male (UNAH); Petoa, 1 male (UNAH); Santa Bárbara, 160 m, 4 males (TCWC); 22 km NNE Santa Bárbara, 4 males, 9 females (TCWC).

The distribution of *B. plicata* extends southward into Central America where it appears to be restricted to the dry western corridor from Guatemala to northwestern Costa Rica (Burt and Stirton, 1961; Jones, 1964a, 1966; Starrett and Casebeer, 1968; Dolan and Carter, 1979). Goodwin (1942a) included this emballonurid in his Honduran report without documentation. Dolan and Carter (1979) cited one specimen from Choluteca. Recently, this bat was reported again in these Pacific lowlands from Valle (Lee and Bradley, 1992). The additional localities that we report place this species in subhumid valleys of western Honduras. The specimen from Parque Nacional La Tigra was collected in dry pine habitat at an elevation around 1500 m. López F. (1981) reported this species from sea level to 1500 m in México. Diurnal roost sites in Honduras included a rock shelter, a mine tunnel, the roof of a church, and the underside of a bridge.

Family Noctilionidae

Noctilio albiventris Desmarest, 1818

This species has been reported from Chiapas (Polaco, 1987), Guatemala (Dolan and Carter, 1979; Dickerman et al., 1981), Honduras (Davis, 1976), and Nicaragua (Goodwin, 1942a; Davis, 1976) in northern Central America. Lee and Bradley (1992) erroneously reported specimens from Olancho, Honduras, as representing the northernmost record for *N. albiventris*.

Family Phyllostomidae

Micronycteris brachyotis (Dobson, 1879)

McCarthy (1987) summarized Middle American records, which included specimens from Veracruz, Oaxaca, Chiapas, northern Guatemala, southern Belize, Nicaragua, Costa Rica, and Panamá. The skin of the only specimen (AMNH) of this species from Nicaragua was reported originally as "Gen. et sp. indet." (J. A. Allen, 1910:112) from Volcán de Chinandega (=Casita), Chinandega. W. B. Richardson obtained this adult bat and prepared it as a skin with skull. Allen did not

recognize it as a *Micronycteris* without the skull. It represented the only museum specimen of *M. brachyotis* other than the holotype in Paris. Allen acknowledged the striking ochraceous coloration of the throat and chest region, which was not mentioned in the original description (Dobson, 1878*b*). Apparently, the skull was disassociated from the skin at some early date and mistakenly cataloged with a juvenile skin of *Carollia brevicauda*. Goodwin (1946) recognized the skull as that of *Micronycteris* but was apparently unaware of the confusion. We assume he reported this mismatched specimen as *M. sylvestris*, in part, because both of these species possess distinctly tri-colored dorsal fur. The holotype (BMNH) of *M. sylvestris* also was the sole specimen of that taxon known at the time, although Thomas (1896) mentioned this general similarity between *C. brevicauda* and *M. sylvestris* in his description of the latter.

Sanborn (1949) recognized the age and identification error of the mismatched skin and skull, and listed only the skull in the description of *M. platyceps*. Although Goodwin and Greenhall (1961) synonymized Sanborn's *platyceps* with *brachyotis*, no further mention has been made of the Nicaraguan specimen. The questionable skin reported by J. A. Allen (1910) was recently located by one of us (McCarthy) and rejoined with its skull.

Micronycteris daviesi (Hill, 1964)

This large, rarely collected *Micronycteris* has been reported in Central America from the Caribbean lowlands of Costa Rica (LaVal, 1977) and Panamá (Hall, 1981). In April 1967, a Texas A & M field party headed by D. C. Carter captured an individual of unknown sex in a mist net at a site 40 km E Catacamas, Olancho, Honduras. The locality is on the Río Perlas where a trail to Valencia (on the Río Patuca) crosses the river. Unfortunately, the bat chewed through a holding bag and escaped. However, it was examined and photographed by R. K. LaVal. A black and white photograph of the specimen has been published (Nowak and Paradiso, 1983:246; Nowak, 1991:276) and the original color slide is stored in the Mammal Slide Library (no. 378) of the American Society of Mammalogists.

Micronycteris minuta (Gervais, 1856)

HONDURAS. Atlántida: Lancetilla, 40 m, 4 males, 1 female (TCWC).

Valdez and LaVal (1971) reported the previous northernmost record of *M. minuta* from mesic forest (500 m) in Departamento de Matagalpa, Nicaragua. Other Central American records are from forested habitats up to 600 m in Costa Rica (Gardner et al., 1970; LaVal and Fitch, 1977) and Panamá (Handley, 1966). An additional Nicaraguan record is documented by a female specimen (UCLA) from the Caribbean drainage at Crique Lecus, 96 km (by road) NW Puerto Cabezas, Zelaya Norte, 60 m.

We anticipated the occurrence of *M. minuta* in eastern Honduras. The specimens from Lancetilla represent a significant range extension northwestward in the country. R. D. Bradley, J. Ensink, and T. E. Lee captured these small *Micronycteris* on 23 June 1983, in moist tropical forest of a botanical garden.

Selected measurements (male, female) of Honduran specimens are: greatest length of skull, 17.15, 17.2; zygomatic breadth, 8.05, 8.1; postorbital constriction, 3.9, 3.9; breadth across molars, 5.35, 5.25; length of maxillary toothrow, 6.0, 6.1; breadth across mastoids, 8.2, 8.35; length of forearm, \bar{x} = 34.0 (n = 4, 33.7–34.2), 33.9.

Micronycteris schmidtorum Sanborn, 1935

McCarthy (1987) summarized the Central American distribution of *M. schmidtorum* in both Pacific and Atlantic drainages. Goodwin (1942a) listed, but did not document, this species from Honduras although Sanborn (1941) had reported one specimen from Copán. Two additional specimens (TCWC) are from 9.6 km W Tela, Atlántida, and 7 km N Santa Bárbara, Santa Bárbara.

Micronycteris sylvestris (Thomas, 1896)

HONDURAS. Colón: Laguna Bacalar, 1 male, 5 females (BMNH).

Middle American records of *M. sylvestris* are scattered. Known localities in México are from Jalisco (Villa-R., 1956), Nayarit (Jones, 1964b), and Colima (Villa-R., 1966) along the dry Pacific coast, and from southern Veracruz (Hall and Dalquest, 1963) in the Gulf drainage. In Central America, it has been recorded from southeastern Nicaragua (Arnold et al., 1983), northwestern Costa Rica (Thomas, 1896; Davis and Carter, 1962a), and coastal Panamá (Handley, 1966).

B. H. Gaskell collected the Laguna Bacalar *M. sylvestris* on 7 October 1982. This is the only reported Honduran locality. Forearm lengths (wet) for five females averaged 41.9 (41.1–43.3); one male measured 40.4.

Macrotus waterhousii Gray, 1843

Guatemala was visited by several early collectors associated with the Muséum National d'Histoire Naturelle, Paris. One French expedition, which stayed from early 1865 until June 1866, was headed by M.-F. Bocourt (Stuart, 1948). Although Bocourt is remembered for his "Verapaz" collection of amphibians and reptiles, he also secured a small collection of mammals that probably originated in the vicinity of Cobán, Alta Verapaz. Four juvenile specimens of *Macrotus* were included among the few bat specimens. G. E. Dobson, while preparing his "Catalogue of the Chiroptera in the Collection of the British Museum" (1878a), examined these *Macrotus* in the Paris museum. He decided that the juveniles represented a larger-sized species of *Macrotus* characterized by having the tail vertebrae extending farther beyond the uropatagial margin and longer ears than in *M. waterhousii*, and by a different noseleaf structure. Dobson (1876) thus described *M. bocourtianus* based solely on Bocourt's specimens. A review of the pertinent literature concerning the taxonomy of *Macrotus* makes it apparent that Dobson was the only researcher to examine these specimens, although *M. bocourtianus* is now generally synonymized with *M. waterhousii* (Rehn, 1904; Anderson and Nelson, 1965). We looked for the original specimens of *M. bocourtianus* only to discover that the species was not listed by Rode (1941) or Carter and Dolan (1978) in their type catalogs. M. Trainer (personal communication) reported that these specimens could not be located in Paris, and we assume they were misplaced, damaged, or loaned long ago. Bocourt's Guatemalan specimens documented the only record of *Macrotus* in Central America.

Lonchorhina aurita Tomes, 1863

HONDURAS. Colón: 3.2 km SE Balfate, 1 male (USNM). Santa Bárbara: Quimistán, 170 m, 1 female (UNAH).

McCarthy (1987) suggested that the Middle American range of this distinctive leaf-nosed species extends northward from Panamá in the Caribbean lowland drainage to southeastern México. McCarthy confirmed that *Lonchorhina* reaches montane elevations, but neglected to cite a Chimaltenango record from the upper

Guatemalan piedmont (Jones, 1966). Felton (1956a) reported this species in El Salvador. The above Honduran records confirm *L. aurita* for the first time in the republic. G. W. Van Hyning obtained the Colón specimen on 14 December 1930, inside a mine tunnel, along with other specimens (FLMNH) of bats. A. Ayala obtained a female from the vicinity of Quimistán on 26 March 1974.

Tonatia evotis Davis and Carter, 1978

BELIZE. Cayo: Central Farm, Baking Pot, 60 m, 1 male (BMNH). Toledo: vicinity Aguacate, 40 m, 2 males, 1 female (CM); 1.2 km E Aguacate, 40 m, 2 males, 1 female (CM); 1.2 km E Aguacate, 30 m, 1 male (CM); 0.8 km NW Blue Creek, 35 m, 2 males (MBS); Crique Negro, Columbia Forest, 160 m, 1 male, 1 female (USNM); Hot Springs, 1.2 km SW Big Falls bridge, Río Grande, 20 m, 2 males (BMNH); Orange Point, s.l., 1 male (FMNH); 1.6 km NNE Salamanca Camp, Columbia Forest, 145 m, 2 males (FMNH); 2.1 km NNE Salamanca Camp, Columbia Forest, 165 m, 2 males (CM).

Sanborn (1941) first reported *Tonatia* from areas north of Panamá based on a specimen (CM) from British Honduras (=Belize). It was identified as *T. amblyotis* (= *silvicola*) and reported as small for this species. Goodwin (1942b) also commented on the overall size of this specimen. Additional material allowed Davis and Carter (1978) to review the *T. silvicola* complex in the northern part of its range. In that paper, they described *T. evotis*, based primarily on smaller size, but did not examine the Belizean specimen. Belize is situated in the Gulf–Caribbean distribution of this large-eared species, which extends from southern Veracruz, Tabasco, Chiapas, southern Campeche, southern Quintana Roo, and El Petén, to Belize, and continues southward in eastern Guatemala and northern Honduras (McCarthy, 1987).

During early 1935, the first biological expedition to the basin and range of the Cockscomb Mountains and adjacent coastal region of Belize was undertaken by E. R. Blake and C. T. Agostini. Although the collecting effort was primarily ornithological, reptiles and mammals were also obtained. The male *T. evotis* reported by Sanborn (1941) was collected on 15 May at Freetown (=Sittee Village), Stann Creek District, and was taken from a house according to the original field catalog. The testes are enlarged and scrotal in the fluid-preserved specimen. Compared with the Belizean specimens reported here, the specimen from Freetown is a smaller individual. Selected measurements given for the Freetown male followed by the mean and range of ten males, unless otherwise stated, in parentheses: greatest length of skull, 24.1 (25.0, $n = 9$, 24.1–25.9); zygomatic breadth, 11.9 (12.3, 11.9–13.1); postorbital constriction, 3.8 (4.0, 3.8–4.2); breadth across molars, 7.55 (8.0, 7.55–8.3); length of maxillary toothrow, 8.1 (8.5, 8.0–9.1); length of mandible, 16.0 (16.0, 15.35–16.5); forearm length, 50.8 (51.3, $n = 14$, 50.2–54.0).

Four of five *Tonatia* were captured (28 April) from an inactive termite nest, located about three meters above ground in a tree, in Toledo District (A. M. Hutson, personal communication).

The absence of light postauricular patches as a character that separates *T. evotis* from *T. silvicola centralis* (Davis and Carter, 1978) appears to be a matter of degree. We examined both holotypes and found that the holotype of *T. silvicola centralis* (TCWC 18774) has more extensive whitish frosting on the dorsum, including the bases of the ears, as the hair tips are longer and lighter than on *T. evotis* (TCWC 17142). A fringe of white hairs near the posterior base of the ears

in *T. evotis* and *T. silvicola centralis* continues to the inside edge of the pinnae. These fringes appear as postauricular patches, being more extensive in *T. silvicola centralis*. The frosting of the ventral fur is extensive in *T. silvicola centralis* with a pure white portion on the throat and chest. The venter in *T. evotis* is only lightly frosted except for a similar, but not as pronounced, whitening in the throat and chest region. The lighter coloration in the postauricular regions and extent of white coloration on the venter and dorsum in *T. evotis* compare favorably with this condition in specimens of *T. silvicola silvicola* from Amazonian Perú (Loreto; TCWC 11700–11701).

Misidentifications of specimens of *T. bidens* with those of the *T. silvicola* complex have been found in museum collections (McCarthy, personal observation). We offer some morphological characters that work well to separate *T. bidens* from *T. evotis* and *T. silvicola centralis*. When viewed posteriorly, the basisphenoid foramina of each taxon is distinctive. The opening is decidedly arched and rounded on *T. evotis*, whereas it is narrow and expanded laterally, although not equally, on *T. bidens* (<1.0) and *T. silvicola centralis* (>1.0). The following structures are more pronounced in *T. bidens*: interpremaxillary foramen is enlarged and obvious anterior to larger palatal foramina; posterior nasal region is more emarginated; basisphenoid pits are relatively deeper with a higher septum; occlusal surface areas of the lower incisors are greater. The first lower premolar on *T. bidens* is symmetrically positioned in the toothrow rather than more labially positioned as in the other *Tonatia*; the occlusal surface of the first lower molar on *T. bidens* appears squarish; upper inner incisors in *T. bidens* are not procumbent and their inside edges are not in contact along the lower two-fifths of their length. Comparatively, the presence of facial hair and a fringe of hair on the inside edges of the ears are more pronounced in *T. bidens*. In northern Central America, white-tipped hairs form a short stripe in *T. bidens* from between the ears on the top of the head to the back of the head that is not found on its congeners.

Mimon cozumelae Goldman, 1914

McCarthy (1987) summarized the Middle American range of this spear-nosed species as extending from northern Oaxaca and southern Veracruz southeastward along the eastern lowlands of Central America. Although 13 localities were reported for *M. cozumelae* in Belize (McCarthy, 1987), only singular localities document it in Guatemala, Honduras, Costa Rica, and Panamá. Additional records for Guatemala and Honduras confirm this Caribbean lowland distribution. Winkelmann (1962), Rick (1968), and McCarthy (1982) reported specimens from Parque Nacional Tikal, El Petén, Guatemala. Three additional Guatemalan specimens include a female (CM) from a cave on Finca Ixobel, south of Poptún, southeastern El Petén, and two individuals (AMNH) from Santo Tomás de Castilla, Izabal. The only Honduran record (Valdez and LaVal, 1971) is from Lancetilla, Atlántida. Further records from Honduras are documented by two specimens (BMNH) from Aguacates, Colón, and four specimens (TCWC) from 40 km E Catacamas, Olancho. There are no records of this species from Nicaragua.

Mimon crenulatum (É. Geoffroy St.-Hilaire, 1810)

HONDURAS. Olancho: 40 km E Catacamas, 500 m, 1 female (TCWC).

Our female was mist-netted on 15 April 1967 by D. C. Carter, R. K. LaVal, and J. T. Webb. It was pregnant with one fetus (crown–rump length, 26). This is the only Honduran record of this species, which has a Middle American range

restricted to the Gulf–Caribbean drainages of Chiapas, Campeche, Guatemala, Belize, Nicaragua, Costa Rica, and Panamá (McCarthy, 1987).

Selected measurements are: greatest length of skull, 23.0; zygomatic breadth, 12.5; postorbital constriction, 4.3; breadth across molars, 8.85; length of maxillary tooththrow, 7.85; breadth across mastoids, 11.8; length of forearm, 51.1 (dry).

Phyllostomus hastatus (Pallas, 1767)

BELIZE. Toledo: near Blue Creek, 35 m, 1 female (WNMU). HONDURAS. Atlántida: Lancetilla, 40 m, 6 males (TCWC), 1 female (UNAH); 14.5 km SW Tela, 30 m, 1 female (TCWC). Colón: Sico, 3 males (BMNH). Cortés: 2 km W La Lima, 40 m, 1 male (TCWC); Omoa, s.l., 1 male (AMNH); 3.2 km W San Pedro Sula, 1 male (TCWC); 3.2 km S San Pedro Sula, 30 m, 1 female (TCWC); 17.6 km S San Pedro Sula, 2 males (TCWC); 9.6 km E San Pedro Sula, 30 m, 2 females (TCWC). Olancho: 6 km SE Catacamas, 1 male (TTU); 19.4 km SSW Dulce Nombre de Culmi, 2 males, 1 female (TTU). Santa Bárbara: Ilama, 120 m, 1 female (TCWC).

Until recently, the sole Honduran record of this large species was based on a male (USNM) that was collected (16 November 1891) by H. W. Perry at Patuca (=Río Patuca, Gracias a Dios; Goodwin, 1942a) in northeastern Honduras. This locality was erroneously reported as in Nicaragua by Lee and Bradley (1992). Eastern Honduras represented the northwestern limit of the distribution for *P. hastatus*, which is well documented from Nicaragua, Costa Rica, and Panamá (Hall, 1981). Marshall et al. (1991) extended its range to eastern Guatemala in the Sierra del Merendón along the Honduran border. Additional specimens from eastern Honduras were collected in Olancho (Lee and Bradley, 1992).

The specimen collected in forest understory near Blue Creek, Belize, on 18 August 1985 by B. J. Hayward, P. Savoie, and J. Serach represents a range expansion north of the Sierra del Merendón and a country record. We document 26 specimens from 13 additional Honduran localities including two localities near the Guatemalan border in northwestern Honduras. McCarthy netted the specimen from Omoa inside a vaulted room of the Spanish coastal fortress of San Francisco de Omoa on 6 August 1988; R. K. LaVal captured a female inside a church bell tower in Santa Bárbara on 30 March 1967. The majority of the Honduran specimens were captured in mist nets. J. V. Mankins shot this species as they roosted inside hollow trunks of cottonwood trees (*Ceiba*) in Departamento de Cortés.

Selected measurements for the female from Belize and the averages (and ranges) for both sexes (ten males, five females) from Honduras are: greatest length of skull, 37.9, 40.4 (39.75–40.9), 39.1 (38.6–39.9); zygomatic breadth, 21.15, 22.6 (21.95–22.95), 21.8 (21.35–21.9); postorbital constriction, 7.2, 7.5 (7.2–7.8), 7.4 (7.2–7.6); breadth across molars, 13.75, 14.2 (13.7–14.55), 13.8 (13.5–14.15); length of maxillary tooththrow, 13.4, 14.0 (13.6–14.2), 13.5 (13.15–13.75); breadth across mastoids, 19.15, 21.3 (20.2–21.85), 20.1 (19.85–20.7); length of forearm, 89.0, 93.5 (90.4–96.8), 91.3 (89.9–92.9). Available weights for nine males and four females from Honduras averaged 127.8 (100.0–142.4) and 107.6 (102.5–117.6) respectively.

Vampyrus spectrum (Linnaeus, 1758)

GUATEMALA. Uncertain locality, 1 male (MNHNG). El Petén: Parque Nacional Tikal, 1 female (USNM). HONDURAS. Gracias a Dios: Río Patuca delta, 1 female (TCWC). Olancho: near Río Talgua, east of Catacamas, 1 female (UNAH);

40 km E Catacamas, 500 m, 1 female (TCWC); 16.5 km (by road) SSW Dulce Nombre de Culmi, 1 female (TTU).

This largest of Neotropical bats has been reported from southern Veracruz, northern Guatemala, southern Belize, northwestern Nicaragua, and southeastward into South America (McCarthy, 1987). Dobson (1878a) listed Guatemala as part of the Central American distribution of this bat, but his report was undocumented by specimens. Alston (1879–82) stated that Dobson claimed he had seen specimens from Guatemala, although Alston knew none was obtained by O. Salvin. The first undoubted Guatemalan record of *Vampyrum* came from the Caribbean lowland in Parque Nacional Tikal, El Petén, where five individuals were identified by sight and photographed (McCarthy, 1987). A female (USNM) from Tikal was obtained by R. G. McLean and S. R. Ubico on 20 May 1984. We were told (G. Ibarra, personal communication) that the *Vampyrum* specimen on exhibit in the Museo Nacional de Historia Natural was obtained over 20 years ago in Departamento de Guatemala near the Puente de las Vacas, approximately 1500 m. We remain uncertain of this locality as no written documentation is associated with this specimen. If accurate, this would represent a rare montane record. Recently, *Vampyrum* was reported from northwestern Honduras (Lee and Bradley, 1992). The additional records reported here document its occurrence in Caribbean lowland habitats of Honduras. A dried carcass (UNAH) was found hanging from a barbed wire fence.

Selected measurements for two females from Honduras are: greatest length of skull, 51.9, 48.8; zygomatic breadth, 24.65, 23.25; postorbital constriction, 7.55, 7.65; breadth across molars, 14.95, 14.8; length of maxillary toothrow, 20.45, 19.55; mastoidal breadth, 22.4, 21.45. Forearms of four females measured 103.8 (wet), 108.4, 106.6, and 107.4.

A specimen supposedly acquired in Nicaragua during the expedition of the H.M.S. Sulphur (Gray, 1844) was cited by Dobson (1878a) and Alston (1879–82). Gray's (1844:19) zoological report of the expedition had an account of *Phyllostomus hastatus* from "Realejo." El Realejo is an old Pacific port in northwestern Nicaragua, near present-day Corinto, where Captain E. Belcher and the Sulfur secured provisions in early April 1837, and mid-November 1838 (Belcher, 1843). Dobson (1878a) reported the "Realejo" specimen as *Vampyrum*. Alston (1879–82) cited Dobson in his *Vampyrum* account. We examined the registers and collection of the British Museum, but found no specimen of *V. spectrum* from Nicaragua. The only documented record of *Vampyrum* in Nicaragua is that of an adult male from the vague locality "Volcán de Chinandega" (=Casita), obtained by W. B. Richardson on 23 August 1908 (J. A. Allen, 1910).

Leptonycteris Lydekker, 1891

Until recently, our taxonomic understanding of *Leptonycteris* was confused. A morphometric analysis (Arita and Humphrey, 1988) revised the systematics of the genus and reviewed the nomenclatural history. Two species, *L. nivalis* (Saussure) and *L. curasoae* Miller represent the genus. The range of monotypic *L. nivalis* extends from the extreme southwestern United States to south-central México, mostly at higher elevations between 1000 and 2200 m. Similarly, *L. curasoae yerbabuenae* Martínez and Villa extends from southern Arizona and New Mexico and Tamaulipas in northeastern México to southern México and northern Central America primarily at elevations below 1800 m (Arita, 1991). In northern Central America, *L. curasoae yerbabuenae* has been reported from the

dry Pacific versant of El Salvador and Honduras (Jones and Bleier, 1974; Lee and Bradley, 1992) and from rain-shadow valleys of western Guatemala (Arita and Humphrey, 1988).

Two historical specimens (BMNH) were reported by Dobson (1878a) as *L. nivalis* from Departamento de Sacatepéquez, Guatemala, where they were obtained by O. Salvin at San Miguel Dueñas (BMNH 1865.5.18.70) and Ciudad Vieja (BMNH 1875.2.27.38). These specimens were not examined by Hoffmeister (1957), Davis and Carter (1962b), Jones (1966), or Arita and Humphrey (1988). In view of the revised range for *L. nivalis* by Arita and Humphrey (1988), the identity of these specimens is in question.

Hill examined these for Hall (1981) using Hall's key. At that time, he decided that these best represent *L. nivalis*. Dobson (1878a) examined the specimens early in their preserved state and listed BMNH 1875.2.27.28 as immature and BMNH 1865.5.18.70 as an adult. We assume Dobson examined and measured the latter bat for his descriptive summary. Dobson stated that the interfemoral membrane was narrow and covered with fine hairs. He made no mention of a distinct uropatagial fringe. These specimens pose a problem because of the length of time they have been stored in alcohol.

Hill recently re-examined these specimens. Specimen BMNH 1865.5.18.70 is a male, but BMNH 1875.2.27.38 has been dissected and it is now difficult to determine its sex. The latter appears to be adult rather than immature as the manal epiphyses are fused. Specimen BMNH 1865.5.18.70 has a moderately developed interfemoral membrane, which in BMNH 1875.2.27.38 is a little wider; in neither is there more than a poorly developed fringe consisting of scattered hairs. This may reflect poor preservation. The skulls remain intact and were not removed due to possible decalcification over time. Relevant external measurements were compared with those in Arita and Humphrey (1988). Specimen BMNH 1865.5.18.70 was measured by P. D. Jenkins, whereas BMNH 1875.2.27.38 was measured both by Hill and by Jenkins. Measurements of BMNH 1865.5.18.70 are: length of forearm, 58.0; length of III metacarpal, 51.2; length of III first phalanx, 16.5; length of III second phalanx, 25.3; length of III third phalanx, 13.2; total III digit length, 106.2. Independent measurements of BMNH 1875.2.27.38 are: length of forearm, 54.2, 54.0; length of III metacarpal, 51.1, 50.5; length of III first phalanx, 14.3, 13.9; length of III second phalanx, 24.5, 24.4; length of III third phalanx, 13.1, 12.4; total III digit length, 103.1, 101.2. When compared with the means and ranges of variation in samples presented by Arita and Humphrey (1988), size alone supports the identification of BMNH 1865.5.18.70 as *L. nivalis*. Measurement of the third finger is variable. The terminal III phalanx is especially difficult to measure as expressed in the two independent measurements taken for BMNH 1875.2.27.38. Dobson (1878a:506) reported his measurement of the third phalanx, apparently of BMNH 1865.5.18.70, as "3rd ph. 0".55," which we interpret as 55 one-hundredths of one inch. If this is so, this equals approximately 14 mm although Dobson's method of measurement is not known. The direct measurements identify BMNH 1865.5.18.70 as *L. nivalis*. We consider the smaller specimen (BMNH 1875.2.27.38) to be *L. curasoe yerbabuenae*.

Anoura geoffroyi Gray, 1838

HONDURAS. El Paraíso: Yuscaran, Montaña Monserrat, 1000 m, 1 male (CM). Francisco Morazán: 16 km NE Talanga, 1115 m, 1 male (TCWC); 19.2 km N Tegucigalpa, 920 m, 7 males (TCWC). Intibucá: La Esperanza, 1660 m, 1

male, 4 females (TCWC). Ocotepeque: 1 km W Nueva Ocotepeque, 840 m, 2 males, 1 female (TCWC). Olancho: 3.5 km E, 3.8 SE Catacamas, 1 female (TCWC); 6 km SE Catacamas, 420 m, 5 males (TTU); 3.8 km SW Dulce Nombre de Culmi, 1 female (TCWC); 16.5 km (by road) SSW Dulce Nombre de Culmi, 450, 1 male (TTU); 6.4 km (by road) S Juticalpa, 4000 m, 1 male (TTU).

This montane and premontane nectar-feeding species apparently has not been reported from Honduras although Goodwin (1942a) included *Anoura* in his Honduran list. Its distribution complements the mountainous regions from western (Sinaloa) and eastern (Tamaulipas) México southeastward throughout Central America (Hall, 1981). Our records from eastern Olancho represent the lowest reported elevations for Central America.

Lichonycteris obscura Thomas, 1895

HONDURAS: Olancho: 16.5 km (by road) SSW Dulce Nombre de Culmi, 2 females (TTU).

These two specimens from Olancho were mist-netted by R. J. Baker and W. J. Bleier on 20 and 22 July 1971, and represent the first Honduran record of this nectar-feeding bat. Central American records of *Lichonycteris* are scattered from southern Belize (Hill, 1985) and eastern Guatemala (Carter et al., 1966), to Nicaragua (Jones et al., 1971), Costa Rica (Gardner et al., 1970; LaVal, 1977), and Panamá (Handley, 1966).

Selected measurements (one female) are: greatest length of skull, 19.65; zygomatic breadth, 8.55; postorbital constriction, 3.9; breadth across molars, 4.5; length of maxillary tooththrow, 6.35; breadth across mastoids, 8.35; forearm length ($n = 2$ females), 32.6, 31.9.

Hylonycteris underwoodi Thomas, 1903

NICARAGUA. Río San Juan: El Castillo, 40 m, 1 female (TCWC); 1 km S El Castillo, 130 m, 2 females (TCWC).

The range of *H. underwoodi underwoodi* includes the Gulf drainage of México (Veracruz, Oaxaca, Tabasco, Chiapas), the Caribbean lowlands of southern Belize and Guatemala, and the mesic coastal regions of Costa Rica and western Panamá (Jones and Holman, 1974; McCarthy and Blake, 1987). Reported elevations range from near sea level to below 2640 m. These three Nicaraguan specimens were collected on 9, 10, and 15 May 1967 by D. C. Carter, and document *Hylonycteris* for the first time in the country.

Averages and ranges of selected measurements of the three females are: greatest length of skull, 22.2 (21.8–22.7); breadth across jugals, 8.6 (8.45–8.65); postorbital constriction, 4.0 (3.9–4.05); breadth across molars, 4.5 (4.35–4.75); length of maxillary tooththrow, 7.6 (7.4–7.9); breadth across mastoids, 8.5 (8.35–8.7); forearm length, 32.5 (32.35–32.75).

The sole published Guatemalan record of this bat is from Departamento de Izabal (Carter et al., 1966). Additional specimens provide records in the Sierra de las Minas [11 km N Santa Cruz, Zacapa (MVZ); near Purulhá, Baja Verapaz (UTACV)] and eastern lowlands [Finca La Unión, about 25 km E Poptún, El Petén (USNM)].

Carollia brevicauda (Schinz, 1821)

Hahn (1907) reported one specimen (USNM) from eastern Honduras as *Hemiderma subrufum*. This adult fluid-preserved specimen with skull extracted was

collected by H. W. Perry on 9 May 1891, on the Río Patuca, Gracias a Dios. Pine (1972) did not mention this specimen in his revision of *Carollia*. We refer the Patuca specimen to *C. brevicauda* as the dorsal pelage is long and individual hairs have distinct bands of contrasting coloration; the proximal portion of the forearm is hairy; the greatest length of the skull is 22.3; and the length of forearm is 39.8. Goodwin (1942a) reported specimens of *C. subrufa* from Muya (=Muye), La Paz, which actually are *C. brevicauda*. Similarly, Guatemalan specimens (AMNH) of *Carollia* from Alta Verapaz (Goodwin, 1955) and Izabal (Goodwin, 1934), which were identified as *C. subrufa*, are *C. brevicauda*.

Carollia castanea H. Allen, 1890

HONDURAS. Copán: Ruinas de Copán, 660 m, 1 male (TCWC).

Pine (1972) reported the northernmost record of this small *Carollia* from Lancetilla, Atlántida, Honduras. Dillard Carter mist-netted the specimen from Copán on 5 March 1967, which marginally extends the range of the species near the Guatemalan border.

Goodwin (1942a) incorrectly reported *C. castanea* in the basin of Sabana Grande, where C. F. Underwood actually obtained specimens of *C. subrufa* from La Piedra de Jesús. Pine (1972) reported these same specimens as *C. brevicauda*.

Vampyressa macconnelli (Thomas, 1901)

NICARAGUA. Zelaya Sur: 4.5 km NW Rama, 100 m, 1 male (TCWC).

We are aware of three records for this small fruit-eating species from Central American moist tropical forest. Handley (1966) reported *V. macconnelli* from near sea level and at about 590 m in Darién and Bocas del Toro, Panamá, and Starrett and Casebeer (1968) reported it from 1116 m in Cartago, Costa Rica. I. F. Greenbaum mist-netted the Zelaya specimen on 25 May 1978, which extends the known range of this species and is the first Nicaraguan record.

Selected measurements are: greatest length of skull, 18.35; zygomatic breadth, 10.45; postorbital constriction, 4.55; breadth across molars, 7.1; length of maxillary tooththrow, 5.85; breadth across mastoids, 9.0; length of forearm, 32.25; weight, 5.0.

Uroderma magnirostrum Davis, 1968

GUATEMALA. Santa Rosa: 10 km S, 14 km E Chiquimulilla, Río Margarita, 700 m, 1 female (TTU).

In Central America, *U. magnirostrum* appears to be restricted to dry Pacific lowlands in El Salvador, Honduras, Nicaragua, and Panamá (Davis, 1968; Jones et al., 1971). Its range continues northward along the coastal plain to Guerrero (Ramírez-P. and López-F., 1979). P. G. Dolan mist-netted the pregnant female from Santa Rosa on 15 July 1977. This specimen confirms the occurrence of this species in Guatemala.

Selected measurements are: greatest length of skull, 23.85; zygomatic breadth, 13.55; postorbital constriction, 5.8; breadth across molars, 9.55; length of maxillary tooththrow, 8.1; breadth across mastoids, 11.5; forearm length, 45.6 (dry).

Artibeus intermedius J. A. Allen, 1897

G. G. Goodwin reported specimens identified as *Artibeus jamaicensis* from Panajachel, Sololá, Guatemala (Goodwin, 1934), and from La Flor Archaga, Francisco Morazán, Honduras (Goodwin, 1942a). These specimens (AMNH)

were re-examined and fit the description (J. A. Allen, 1897; Davis, 1984) of *A. intermedius*.

Ectophylla alba H. Allen, 1892

This Central American endemic is documented along the Caribbean corridor from eastern Honduras to western Panamá (Timm, 1982; Benshoof et al., 1984). The range of the white bat extends from near sea level to above 730 m in primary forest where it is associated with *Heliconia* stands, which it utilizes as diurnal roosting sites.

The description of *E. alba* was based on a fluid-preserved specimen without a skull, which was obtained by C. H. Townsend and "believed to be from the vicinity of the Segovia River [=Río Coco], Eastern Honduras" (H. Allen, 1892: 441). Miller and Kellogg (1955) restricted the type locality to Departamento de Comarca de El Cabo (=Zelaya Norte), northern Nicaragua. This emendation has been accepted since without question (Timm, 1982; Jones et al., 1988).

Ectophylla alba was included in a preliminary checklist of Nicaraguan mammals (J. A. Allen, 1910:91) based on specimens from the "Segovia River." Allen, in the same paper, quoted from correspondence with C. H. Townsend about his travels in Honduras including his visit to the Río Segovia (=Río Coco). In a footnote, Allen made a puzzling error and placed Townsend in Nicaragua. We examined Townsend's original handwritten letter to Allen, dated 11 April 1910, and found that Allen misinterpreted Townsend's original comment that "all collecting done at Truxillo [=Trujillo] on the N. coast was within a few miles of the town." J. A. Allen (1910:90) apparently assumed that "N." referred to "Nicaragua." Allen reported that Townsend's field work along the Río Coco was restricted to open pine habitat adjacent to "jungle" vegetation along the river and above an apparent locality referred to as "Soohee" (or possibly Hoohee). Neither Ridgeway (1888) nor True (1888) mentioned that Townsend travelled to the Nicaraguan side of the Río Coco and considered all of his specimens Honduran. Stone (1932:293) also communicated with Townsend and stated that Townsend "did most of his work in the low country adjacent to it [the river], not penetrating far into the pinelands above." J. A. Allen (1910:112) contradicted himself by listing the general type locality for *Ectophylla alba* as "from Segovia River, Honduras."

We are unaware of whether information about the Townsend fieldwork influenced Miller and Kellogg (1955) to change the type locality for this species. One strong possibility may have been their choice of political maps. We believe Miller and Kellogg (1955) recognized the international boundary claimed by Nicaragua, which incorporated both banks of the Río Coco and adjacent Honduras. Honduras disputed this claim and, in the final decision, the International Court of Justice, The Hague, on 18 November 1960, restricted the boundary between the countries as along the Río Coco (Johnson, 1964). We conclude that the type locality was originally placed correctly on the Honduran side of the Río Coco.

Several years following the publication of the original description, an additional specimen (BMNH) of *Ectophylla* was used to describe the skull and dentition (H. Allen, 1898). This bat was shot by W. B. Richardson in the vicinity of "San Emilio," which was reported as located on the southern shore of Lago de Nicaragua by H. Allen (1898). This locality was also reported by Thomas (1896). Confusion arose over the location of Richardson's collecting site when Casebeer et al. (1963) stated that "San Emilio" was actually in Costa Rica and approximately 10 km

east and 15 km south of the southeastern corner of Lago de Nicaragua. In 1963, however, it was possible that a settlement by that name no longer existed. Also, San Emilio is a fairly common name. T. R. Howell (1964; personal communication) clarified the location of this important collecting site. The majority of Richardson's birds from San Emilio are in the Field Museum of Natural History. In that collection, the locality is recognized as being on the south-central shore of Lago de Nicaragua in Departamento de Rivas. Richardson recorded "San Emilio, (Rivas)" on his bird labels. Howell also located San Emilio on an undated map published in Germany. From that map, he judged that the locality was situated in Nicaragua about 6 km east (=southeast) of Cárdenas and 4 km west (=northwest) of Orosí. Hall (1981) cited Casebeer et al. (1963) for his range map of *E. alba*. Timm (1982) acknowledged Howell (1964), plotting Richardson's locality accordingly. Recently, Timm et al. (1989) claimed this record as Costa Rican without further explanation. We accept Howell's determination.

Our re-evaluation of the preceding Townsend and Richardson localities document these old records of *Ectophylla* as from Honduras and Nicaragua, respectively. *Ectophylla alba* has been reported since from eastern Honduras (Benshoof et al., 1984) and eastern Nicaragua (Greenbaum and Jones, 1978).

Chiroderma salvini Dobson, 1878

This species has been reported from Central America in upland regions (580–1436 m) of Guatemala (Carter et al., 1966), El Salvador (Hellebuyck et al., 1985), Honduras (Sanborn, 1941; Goodwin, 1942a; Handley, 1965; Carter et al., 1966; LaVal, 1969), Costa Rica (Goodwin, 1946; Wilson 1983; Timm et al., 1989), and Panamá (Handley, 1966). The only Guatemalan record is from Villalobos, 13 km S Guatemala City (Carter et al., 1966) in the central highlands. Two further specimens (FMNH, TCWC) are from the vicinity of San Pedro Yepocapa, Chimaltenango, and from xeric habitat above the Río Salamá, 2 km SE Salamá, Baja Verapaz. A historic specimen (SMNS) apparently was obtained in 1885 from an unspecified locality in the vicinity of "Volcán de Fuego."

Chiroderma villosum Peters, 1860

HONDURAS. Atlántida: 11.2 km E La Ceiba, 30 m, 1 male, 1 female (TCWC). Choluteca: 18.4 km S Choluteca, 50 m, 1 female (TTU). Francisco Morazán: 0.5 km SE Sabana Grande, 1000 m, 1 male, 1 female (TTU). Intibucá: near Quiraguira, 1 ? (UNAH). Olancho: Dulce Nombre de Culmi, 1 ? (UNAH); 16.5 km (by road) SSE Dulce Nombre de Culmi, 1 male (TTU). Valle: 4.2 km W, 17.3 km S Jicaro Galán, 19 males, 8 females (TCWC); 16 km SSW Nacaome, 30 m, 6 males, 1 female (TTU).

This species is widespread and occurs from lowland to mid-elevational regions of southeastern México southeastward throughout Central America, although it has remained unreported from Honduras (McCarthy, 1987). Goodwin (1942a) did not list this species. The occurrence of *C. villosum* in both dry and mesic regions of Honduras is documented here by eight records.

Hellebuyck et al. (1985) first reported this species in western El Salvador. Additional specimens (TTU) from El Salvador were listed by Owen (1987) without locality data. These ten examples were obtained at a locality 4.8 km NW La Herradura, La Paz. One further La Paz record is a male (CM) from about 5 km NW San Luis Talpa.

Enchisthenes hartii (Thomas, 1892)

McCarthy and Bitar (1983) first reported this species in Guatemala from the central highlands, approximately 4.8 km NE Antigua Guatemala, Sacatepéquez. This montane species is restricted in Central America to the uplifted regions of Chiapas–Guatemala, El Salvador, Honduras and Costa Rica–Panamá, where the majority of specimens were obtained from localities above 1500 m (McCarthy and Bitar, 1983; Hellebuyck et al., 1985). A male specimen (USAC) was collected at about 1600 m, 2 km E, 2.3 km S Purulhá, Baja Verapaz, in the western Sierra de las Minas.

Owen (1987) analyzed the phylogenetic relationships among fruit bats of the subfamily Stenodermatinae. The smaller species of the *Artibeus* complex were recognized as a natural assemblage and placed under the available generic name *Dermanura* Gervais. Although the exact relationship of *Enchisthenes* to this *Dermanura* group remains unclear from Owen's results, he synonymized *Enchisthenes* with *Dermanura* based on his attempt to stabilize the generic allocation for this bat. Koopman (1978) previously replaced *Enchisthenes* with *Artibeus*, in which Thomas (1892) described the species. Koopman's synonymy was followed by Anderson et al. (1982) and Handley (1987), but none justified this position. At present, the more stable decision is to retain *Enchisthenes*, which has been in the literature longer than either *Artibeus* or *Dermanura*.

Family Natalidae

Natalus stramineus Gray, 1838

HONDURAS. Comayagua: Comayagua, 580 m, 1 male (TCWC). Copán: 6 km ESE Copán, 900 m, 6 males, 13 females (TCWC). El Paraíso: 4.8 km S Guinope, 1280 m, 1 male (TCWC). Francisco Morazán: Valle de Angeles, 1 ? (UNAH); 9.6 km N El Zamorano, 10 males (TCWC). Islas de la Bahía: Isla de Utila, 3.2 km N Utila, 7 m, 3 males, 1 female (TCWC). La Paz: Cueva del Viejo, 3.2 km W La Paz, 545 m, 2 males, 2 females (TCWC). Olancho: 40 km E Catacamas, 500 m, 1 male (TCWC); Río Tinto, San José, 350 m, 2 males, 1 female (TCWC). Santa Bárbara: 2 km S San Nicolás, 660 m, 1 male, 10 females (TCWC); 12 km N Santa Bárbara, 1 male (TTU).

The range of the funnel-eared bat extends from northern México into South America (Jones et al., 1988). Goodwin (1942a) provided an account of *Natalus* without documentation in his report on Honduran mammals. This species evidently is uncommon in Nicaragua, Costa Rica, and Panamá (McCarthy, 1987). This does not appear to be the situation in Honduras, however, where our 11 localities represent the first published records.

Family Vespertilionidae

Myotis albescens (É. Geoffroy St.-Hilaire, 1806)

GUATEMALA. Izabal: Zapotillo, 4.8 km E El Estor, 1 male (FLMNH).

LaVal (1973a; 1977), Dolan and Carter (1979), and Medellín et al. (1986) summarized the Middle American localities (Veracruz, Chiapas, Honduras, Nicaragua, Costa Rica, Panamá) for this species. The scattered records suggest that *M. albescens* occupies the moist slopes along the Gulf–Caribbean corridor and occurs at least as far north on the Pacific versant as southern Honduras (Departamento de Choluteca). The few records from north of Panamá are at lowland elevations from near sea level to 550 m. This Izabal record documents the occurrence of the species in Guatemala for the first time.

Dobson (1878a) listed *M. albescens* from Guatemala under the generic name *Vespertilio*, based on specimens (BMNH, USNM) obtained by O. Salvin at Ciudad Vieja, Sacatepéquez. This series was re-examined by Miller and Allen (1928) and found to represent *M. velifer*. Our Guatemalan specimen was mist-netted by H. Popenoe in February 1961, over a stream north of Lago Izabal. The testes were descended and enlarged with the caudal portions of the epididymides projecting into the interfemoral membrane.

We examined and measured specimens of *M. albescens* from Chiapas (TCWC, USNM), Honduras (TTU), and Nicaragua (TCWC, UMMZ) and compared their measurements with those of our Guatemalan specimen and with measurements reported by LaVal (1973a) and Jones et al. (1971). The Izabal male is large in comparison with specimens from northern Central America. Selected measurements of the Izabal male are compared with the averages (ranges in parentheses) for males, followed by those for females, from Chiapas, Honduras, and Nicaragua: greatest length of skull, 14.5, 13.7 ($n = 3$, 13.25–14.25), 14.4 ($n = 3$, 14.2–14.9); zygomatic breadth, 9.05, 8.5 ($n = 5$, 8.2–8.75), 8.75 ($n = 3$, 8.55–9.0); postorbital constriction, 3.75, 3.85 ($n = 8$, 3.75–4.15), 3.9 ($n = 3$, 3.75–3.8); breadth across molars, 5.35, 5.3 ($n = 8$, 5.15–5.45), 5.5 ($n = 3$, 5.2–5.7); length of maxillary toothrow, 5.1, 4.8 ($n = 8$, 4.4–4.95), 5.1 ($n = 3$, 4.9–5.2); breadth across mastoids, 7.15, 7.2 ($n = 8$, 7.0–7.4), 7.4 ($n = 3$, 7.3–7.65); length of forearm, 37.1 (wet), 34.4 (dry, $n = 9$, 33.7–35.8), 36.05 (dry, $n = 3$, 35.85–36.15).

The braincase of our skull is inflated and smoothly rounded. Cingula are weakly developed or lacking altogether on the cheekteeth. The number of premolars is irregular with the upper left P^3 and the lower right P_3 missing, whereas the lower left P_3 is fused with P_4 . LaVal (1973a) found only one example with a missing P^3 among a sample of 60 specimens. A right upper P^3 is missing in a male (TCWC 24091) from Nicaragua. Although our fluid specimen is faded, the white-tipped hairs on the dorsum are clearly evident.

Myotis californicus (Audubon and Bachman, 1842)

The only Central American specimen of *M. californicus* was mist-netted in Antigua Guatemala, Sacatepéquez, Guatemala (McCarthy and Bitar, 1983). Two additional specimens (TCWC) from 1 km NE Aguacatán, Huehuetenango, 1620 m, further document this species in the central highlands.

Myotis keaysi J. A. Allen, 1914

LaVal (1973a) based his description of the subspecies *M. keaysi pilosatibialis* on a large number of specimens from localities ranging from Tamaulipas, México, south to Venezuela and Trinidad. He selected an adult male as the holotype from a large series collected at 1 km W Talanga, Francisco Morazán, Honduras, 750 m. This remains the only reported locality for *M. keaysi* in the country. A second Honduran locality is documented by a single non-lactating female (AMNH) collected at Santo Domingo, approximately 5.5 km ESE Cuyamel, about 700 m in the Sierra de Omoa.

Eptesicus fuscus (Palisot de Beauvois, 1796)

Although the big brown bat is widespread in México (Jones et al., 1988), its abundance appears to decrease southeastwardly along the Central American isthmus. *Eptesicus fuscus* is known from higher elevations in Guatemala (Dobson, 1878a; Goodwin, 1934, 1955; Jones, 1966), Honduras (Goodwin, 1942a), El Salvador (Burt and Stirton, 1961), Costa Rica (Goodwin, 1946), and Panamá

(Handley, 1966). Two Guatemalan specimens (AMNH) are unusual in that both are from localities in the Gulf lowlands of El Petén. Goodwin (1955) reported these specimens (as *E. fuscus*) which were collected by T. Larson in 1946 from Flores and La Libertad, both below 220 m. Upon re-examination of these specimens, McCarthy found that the juvenile *Eptesicus* from Flores is *E. furinalis*. The adult specimen from La Libertad is *E. fuscus*. The smaller species *E. furinalis* is common in the lowlands of Guatemala (Rick, 1968; Davis, 1965; Dickerman et al., 1981).

Pipistrellus subflavus (F. Cuvier, 1832)

HONDURAS. Olancho: 16.5 km (by road) SSW Dulce Nombre de Culmi, 1 male (TTU).

The known range of *P. subflavus veraecrucis* extends from the Gulf lowlands of Veracruz (Hall, 1981) to the Caribbean lowlands of Izabal, Guatemala (Carter et al., 1966), and Atlántida, Honduras (Rinker, 1948). The specimen from Olancho extends the range of this species about 185 km ESE from Jilamo, Atlántida. W. J. Bleier captured this bat on 22 July 1971.

Selected measurements of the male from Olancho, followed by the average for three females (UMMZ) from Atlántida (in parentheses) are: greatest length of skull, 12.15 (12.3); zygomatic breadth, 7.5 (7.55, $n = 2$); postorbital constriction, 3.35 (3.35); breadth across molars, 4.75 (4.85); length of maxillary toothrow, 3.7 (3.9); breadth across mastoids, 6.5 (6.6); forearm length, 31.4 (dry) (32.8, wet).

Lasiurus intermedius H. Allen, 1862

The distribution of this species extends southeastward from México to Guatemala, Belize, El Salvador, and Honduras (McCarthy, 1987). The only published Guatemalan record is from near Aguacatán, Huehuetenango (Carter et al., 1966). Two specimens (TCWC) from about 5 km W El Progreso, El Progreso, and in the Pacific coast at 8 km NW Puerto de San José, Escuintla, further document the distribution of *L. intermedius* in Guatemala.

Family Molossidae

Tadarida brasiliensis (I. Geoffroy St.-Hilaire, 1824)

HONDURAS. Francisco Morazán: Montañas de San Juancito, above Río Choluteca at San Juan de Flores, 1740 m, 2 males (ANSP). Ocotepeque: Belén Gualcho, 1 male (UNAH).

Central American records of this migratory free-tailed bat are scattered in Guatemala (Jones, 1966), Costa Rica (Goodwin, 1946; Starrett and de la Torre, 1964; Dolan and Carter, 1979), and Panamá (Handley, 1966) at relatively high elevations (>1200 m). J. T. Emlen and C. B. Worth collected the specimens from Montañas de San Juancito on 1 August 1930. The recorded elevation of approximately 1740 m places the collection site somewhere below the cloud forest level and above the pine forests on the northeastern slope of this range (Stone, 1932). M. Villeda and R. Sánchez obtained the specimen from Ocotepeque on 11 July 1975. These specimens are the first records of this species from Honduras.

Averages (and ranges) for selected cranial measurements of the three males are: greatest length of skull, 16.4 (16.1–16.8); zygomatic breadth, 9.6 (9.6–9.7); postorbital constriction, 3.7 (3.65–3.8); breadth across molars, 6.6 (6.4–6.85); length of maxillary toothrow, 5.7 (5.5–5.85); breadth across mastoids, 9.2 (9.05–9.3).

Nyctinomops laticaudatus (É. Geoffroy St.-Hilaire, 1805)

HONDURAS. Yoro: Río Aguán, 8 km W Yoro, 680 m, 1 female (TCWC).

This species is well documented in the lowlands of Guatemala (Alston, 1879–82; Murie, 1935; Goodwin, 1955) and Belize (Murie, 1935; Silva-Taboada and Koopman, 1964). Single lowland records have been reported from El Salvador (Felten, 1956*b*) and Nicaragua (Jones et al., 1971). Handley (1966) reported three Panamanian records. R. K. LaVal collected (18 March 1967) the specimen reported here, a pregnant female (one fetus; crown–rump length, 26), over the Río Aguán. This specimen constitutes the only record of *N. laticaudatus* for Honduras.

Jones et al. (1971) reported the only record of *N. laticaudatus* from Nicaragua. Hall (1981) mapped this record from Potosí, Chinandega, but also reported one specimen of *Eumops bonariensis* from the same locality. Jones recalled that only one molossid specimen was obtained at that site. During the late 1970s, R. M. Timm (personal communication) discovered that Jones' specimen (KU) was misidentified, and confirmed it as *E. bonariensis*. Hall (1981) incorporated this correction but failed to delete the Potosí locality for *N. laticaudatus*. Hall (1981) thus constitutes the first report of *E. bonariensis* from Nicaragua, whereas the Jones et al. (1971) report of *N. laticaudatus* is negated and the species should be removed from the Nicaraguan checklist (Jones and Owen, 1986). We follow Freeman (1981) in using *Nyctinomops* in place of *Tadarida* for the species *laticaudata*.

Eumops hansae Sanborn, 1932

This small mastiff bat has been reported from scattered regions in southern Brazil–eastern Bolivia, Amazonian Brazil, Venezuela–Guianas, and northern Perú (Eger, 1977; Graham and Barkley, 1984; Ochoa et al., 1988; Ibáñez and Ochoa, 1989; Brosset and Charles-Dominique, 1990). Two specimens have been documented from eastern Panamá and southern Costa Rica (Handley, 1966; Gardner et al., 1970) and Alvarez-Casteñeda and Alvarez (1991) reported this species in the coastal plain of Chiapas, México. Recently, one specimen from northwestern Honduras was erroneously reported as the northernmost record for this species (Lee and Bradley, 1992).

Molossus aztecus Saussure, 1860

C. F. Underwood obtained two specimens (AMNH) in March 1937, at El Manteado and Los Encuentros, La Paz, Honduras. Goodwin (1942*a*) listed El Manteado and Los Encuentros as about 6.4–8 km and 10 km, respectively, northwest of San José. These specimens were reported originally as *Molossus bondae* (Goodwin, 1942*a*). LaVal (1977) examined them and disputed Goodwin's identification, but did not offer an opinion as to their identity. The dorsal pelage of *M. rufus*, *M. pretiosus*, and *M. bondae* is short and blackish with only a slightly paler coloration, if any, basally (Dolan, 1989). One of the specimens from La Paz is in blackish-brown pelage and matches the coloration of specimens of *M. aztecus* (TCWC) from Matagalpa, Nicaragua. The second specimen is reddish-brown. Both possess basal bands of white or buffy white on the dorsal hairs. The dorsal pelage of both is longer than that of specimens (TCWC) of *M. bondae* from Gracias a Dios, Honduras.

Dolan (1989) demonstrated that in species of *Molossus*, males average larger than females in almost all measurements, and that *M. bondae* is larger than *M. aztecus*. Averages of selected measurements for the two La Paz males, *M. aztecus*, followed by those of three female *M. bondae* (in parentheses) are: greatest length

of skull, 18.35 (19.3); zygomatic breadth, 11.75 (12.4); breadth across molars, 8.0 (8.7); breadth across canines, 4.65 (4.8); length of maxillary toothrow, 6.15 (6.8); forearm length, 38.25 (44.15). The skulls of the La Paz specimens have broad rostra, and their measurements agree with those given by Dolan (1989) for two male *M. aztecus* from Matagalpa, Nicaragua. The shape of the upper middle incisors are indeterminable due to wear and damage. Dolan did not examine these specimens, nor did she recognize their upland localities, as she assigned them to *M. molossus*. Goodwin (1942a) reported El Manteado and Los Encuentros as at approximately 3000 ft in elevation. Dolan considered *M. aztecus* as a montane species, occurring above 1500 ft. We follow Dolan (1989) for the recognition of *aztecus* as a distinct species.

Dolan (1989) mistakenly reported that Murie (1935) recovered the remains of a *M. aztecus* from a falcon in Guatemala. This specimen originated from a locality in the Mountain Pine Ridge region of Belize. Dolan did not examine this Belizean specimen (UMMZ), but arbitrarily assigned it to *M. molossus* based on the general elevation of the area. McCarthy could not locate the remains of this specimen, which may have been discarded (P. Myers, personal communication).

THE SALVIN AND GODMAN CONNECTION AND OTHER HISTORICAL COMMENTS

The first significant collection of bats from northern Central America was amassed through the efforts of O. Salvin and F. D. Godman during their long-term study of the biology of Central America. The reports of many specialists were accumulated in 63 volumes of "Biologia Centrali-Americana," which covered the majority of known animal and plant groups. Salvin made four visits to Guatemala: December 1857–June 1858; spring 1859–April 1860; August 1861–early 1863; and mid-1873–March 1874. Godman accompanied him during his third and most extensive expedition. During these stays, various people in Guatemala were enlisted to collect and prepare biological specimens, especially ornithological material. Local collectors continued to obtain and ship specimens to England during Salvin's absence and following his last expedition (Godman, 1915; Griscom, 1932).

All of the bats in Salvin's collection were obtained in Guatemala, except for one specimen of *Artibeus jamaicensis* from Belize (McCarthy, 1987). He did not visit El Salvador, Honduras, or Nicaragua. Dobson (1878a) and Alston (1879–82) summarized data on the majority of his specimens. E. R. Alston was enlisted to complete a treatment of Central American mammals for "Biologia Centrali-Americana." An appendix to this volume consisting of additional records was near completion when Alston suddenly died in 1881. O. Thomas included further specimens to finish that account.

G. C. Champion was employed by Salvin and Godman principally to collect insects in Guatemala in the period from 1879 to 1881. Among the species included by Thomas in the Alston supplement were specimens of the bats *Diclidurus albus* and *Choeronycteris minor* collected by Champion. The latter specimen was subsequently described (Thomas, 1903) as a new species, *Choeroniscus godmani*, in honor of Godman. The BMNH registers document additional bat specimens from Champion. Original identifications in the 1881 register record specimens of *Glossophaga*, *Lasiurus*, *Rhogeessa*, *Nyctinomops*, and *Eumops* from San Jerónimo (Departamento de Baja Verapaz) and Cahabón (Departamento de Alta Verapaz).

Of these, only a specimen of *Artibeus lituratus* preserved in alcohol has been located.

Examination of the Salvin and Godman specimens in the fluid collection at the British Museum proved difficult. Few identification changes have been noted in the museum registers. For example, a specimen entered as *Rhinolophus* in 1875 may retain that identification, which does not reflect its actual identity as *Micronycteris*. Furthermore, it is possible that specimens were damaged or lost while stored in Bloomsbury before the Natural History Museum was moved to South Kensington in 1883.

Accurate accounting of the Salvin and Godman material is made difficult by the fact that some specimens may have been dispersed. As one example, R. F. Tomes obtained specimens from Salvin and Godman, which eventually were returned to the museum in 1907 when Tomes' collection was accessioned there. Salvin completed three trips to Guatemala by mid-1863, but the mammal specimens from these expeditions were not accessioned into the museum until 1865. Tomes (1861) published a list of mammals collected by Salvin at San Miguel Dueñas. There was also an exchange with G. E. Dobson in November 1875, which included two bats from the Salvin collection.

Another name associated with Guatemalan mammalogy in "Biologia Centrali-Americana" is that of F. C. Sarg. Sarg was a German immigrant whose family established a coffee plantation in the vicinity of Cobán, Alta Verapaz (Stoll, 1886). Sarg had an active interest in natural history and sold specimens to Salvin and Godman, besides providing observations on a variety of mammals. He continued to collect specimens after Alston's volume was published, two of which were the basis for the description (Thomas, 1904) of the Middle American endemic species, *Balantiopteryx io*.

Some of Sarg's mammals were deposited in Museum für Naturkunde der Humboldt, Berlin. One bat, *Diclidurus albus*, was reported (Alston, 1879–82) from the Berlin collection. A list of 13 Guatemalan bats (R. Angermann, personal communication) from the Berlin Museum included the *Diclidurus*. There is no indication that specimens in the remainder of this list were collected by Sarg. Eight of these specimens were sold to the Berlin Museum by G. Schneider, a natural history trader in Basel. Dr. Angermann pointed out that a Berlin trader, H. Rolle, handled the Sarg mammals, which appear to have represented single specimens of selected species.

McCarthy discovered Guatemalan mammals collected by Sarg in the Staatliches Museum für Naturkunde, Stuttgart. We learned that the Sarg family apparently originated somewhere in the region of Stuttgart (F. Dieterlen, personal communication), which may explain why his collection was sent there. Specimens of bats were received in Stuttgart between 1878 and 1887. McCarthy examined the collection of 30 fluid-preserved specimens, many without locality data, and identified 17 species: *Diclidurus albus*, *Noctilio leporinus*, *Pteronotus davyi*, *Micronycteris megalotis*, *Glossophaga soricina*, *Choeronycteris mexicanus*, *Sturnira lilium*, *Artibeus jamaicensis*, *Platyrrhinus helleri*, *Chiroderma salvini*, *Dermanura phaeotis*, *Centurio senex*, *Natalus stramineus*, *Myotis nigricans*, *Lasiurus blossevillii*, *Eumops auripendulus*, and *Promops centralis*.

Field collecting in Central America ended for Salvin and Godman in 1898. A. W. Anthony undertook the next significant collecting effort in Guatemala from May 1924 to October 1928. Anthony was a veteran ornithologist who sold birds

to the American Museum where L. Griscom published a distributional study of the Guatemalan fauna (Griscom, 1932). Anthony also secured a representative mammal collection for his son, H. E. Anthony, who was Curator of Mammalogy, at the same institution. Guatemalan specimens of 17 species of bats collected by Anthony were reported by Goodwin (1934).

While enroute to Guatemala, Salvin and Godman travelled to Belize City where they transferred to another ship after a few days and proceeded down the coast to Izabal. In 1862, Salvin travelled through the Petén, from Cobán to the Belize River and on to Belize. It was his intention to continue on to Izabal in order to return to the interior of Guatemala, but he was delayed because of the unavailability of a boat. To occupy this time, he explored the bird fauna of the offshore islands and reef associations (Salvin, 1864; Godman, 1915). One male bat, *Artibeus jamaicensis* (BMNH), was secured from Half Moon Caye. There are no additional bat specimens from Belize in the Salvin collections. This specimen was listed by Dobson (1878a:520) and Andersen (1908:266) as from "Honduras," although this was a term generally used in reference to the region that extends from southern Quintana Roo, México, southeastward to northern Honduras (McCarthy, 1987).

The first documentation of bats from Belize resulted from a venture by David Dyson to the British settlement in Honduras. Dyson was a young naturalist, about 21 years old, when he travelled to Belize under the sponsorship of the Thirteenth Earl of Derby, the British Museum, Hugh Cuming of London, The Zoological Society of London, and the Manchester Botanical Gardens. A letter from Dyson's brother to the Earl of Derby is in the archives of the Merseyside Museum, Liverpool. This states that Dyson left for Belize on the Tuesday before 20 September 1844. The elder Dyson notified those (subscribers) who were supporting his brother's venture of his departure and his hope for success. Dyson arrived in Belize on 3 November 1844 and made general natural history collections in the area until late 1845 (Jackson, 1908). With his field efforts, natural history studies of present-day Belize began. Among his specimens (BMNH) are the bats *Sturnira lilium* and *Rhogeessa tumida* (McCarthy, 1987). Hugh Cuming was a shell collector and an agent, who apparently bought and sold Dyson specimens, but he did not accompany Dyson to the settlement as implied by McCarthy (1987).

Godman (1915) stated that he and Salvin were not interested in conducting fieldwork or supporting collectors in El Salvador. Even during their time they considered El Salvador to be overpopulated with much of the land under cultivation. Godman failed to mention that W. B. Richardson collected birds for them in El Salvador from February to April 1891 (Dickey and Van Rossem, 1938). We know of no mammal specimens. They believed that the flora and fauna there was similar to that of nearby Guatemala and Honduras, although Richardson collected some unique bird specimens. Captain John M. Dow, who commanded the coastal steamer "Guatemala," obtained a series of *Myotis* near Volcán Izalco prior to 1860. These appear to represent the first bat specimens (ANSP) from El Salvador (Burt and Stirton, 1961).

G. F. Gaumer was a U.S. citizen and long-time resident of Izamal, Yucatán. He was an avid naturalist who made considerable collections of mammals, birds, and insects from the peninsula. Gaumer was visited briefly by Godman during the latter's field work in México in 1887 and 1888 (Godman, 1915). On behalf of Salvin and Godman, Gaumer investigated the bird faunas on the coastal islands along the Yucatán Peninsula and in the Bay of Honduras. To our knowledge, the

first reported bat specimens from Honduras were obtained by Gaumer in 1886 and 1887 on the island of Roatán (Thomas, 1888). His small collection in the British Museum included specimens of *Saccopteryx bilineata*, *Glossophaga soricina*, *Artibeus jamaicensis*, and *Molossus molossus*. Three specimens (*G. soricina* and *A. jamaicensis*) were transferred from London at an undetermined time to the Biological Museum, University of Toronto. Eventually, these were incorporated in the collections of Royal Ontario Museum at its inception in 1901 (W. Hlywka, personal communication).

It appears that Gaumer was in the Bay Islands during September 1887 when C. H. Townsend visited Roatán (Monroe, 1968). Townsend was in the joint service of the U.S. Fish Commission and the U.S. National Museum. His primary interest was to investigate the bird fauna of the Swan Islands and the Mosquitia Coast of Honduras. A substantial mammal collection was made that included the few bats mentioned in the preceding accounts, including the holotype of *Ectophylla alba*.

The first extensive mammal collection from Honduras was secured by C. F. Underwood. As a young man, Underwood left England in 1889 for Costa Rica where he was engaged in taxidermy and collecting with the Museo Nacional de Costa Rica. Bat specimens were purchased from Underwood by the British Museum in 1895. These included the holotypes of *Micronycteris sylvestris* and *Hylonycteris underwoodi* (Thomas, 1896, 1903). In early 1931, Underwood moved from Costa Rica to Honduras, where he collected birds and mammals until early 1938, when he returned to Costa Rica (Monroe, 1968). Underwood's mammal collections were purchased during this period by the American Museum. Descriptions of the bats *Phylloderma stenops septentrionalis*, *Sturnira hondurensis*, and *Eumops underwoodi* were based on Underwood specimens (Goodwin, 1940).

W. B. Richardson was the most important early mammal collector in Nicaragua. As a young man from Boston, he collected birds for Salvin and Godman in México, where he joined Godman in 1887. He continued to work for his British sponsors in Guatemala in 1889 and 1890. Richardson's Nicaraguan fieldwork was carried out at intervals after he settled in Matagalpa, Nicaragua, in 1891 to grow coffee. Bird collecting also took him to Honduras briefly. Financial support for his collecting efforts was suspended shortly before Salvin's death in 1898. Richardson approached the American Museum that same year for support to collect birds. Sporadic collections were made in the period 1904 to 1909, depending on Richardson's time and availability of funds from New York. His serious mammal collecting began in 1906 (J. A. Allen, 1908, 1910). Fieldwork by Richardson for the American Museum continued in Colombia and Ecuador (1911–13), and Panamá (1915). Richardson resumed collecting in Nicaragua during the first half of 1917 (T. R. Howell, personal communication).

Interestingly, Godman (1915) did not mention Richardson in his abbreviated account of the fieldwork undertaken in Nicaragua, although he included Charles W. Richmond. Although Richmond was not a collaborator of Salvin and Godman, he obtained a significant bird collection from the Caribbean lowlands of southeastern Nicaragua. Richmond was accompanied by his brother, W. L. Richmond, and G. E. Mitchell during the period 1 February 1892 to 19 January 1893. A description of the region, his collecting itinerary, and accounts of the birds were provided by Richmond (1893). In addition to birds, a small number of bats was deposited by Richmond in the U.S. National Museum. These included *Rhynchonycteris naso*, *Saccopteryx bilineata*, *Lichonycteris obscura*, *Myotis albescens*, *Myotis riparius*, and *Eptesicus furinalis*. An important collecting locality was the

International Planting (I. P.) Company's plantation along the Río Escondido, which was estimated to be approximately 50 mi by river west of Bluefields. Jones and Engstrom (1986) stated the I. P. plantation was located 3 km S and 13 km E Rama. G. E. Mitchell acquired three specimens of *Thyroptera discifera* there. These represent the only record of the species on the Central American isthmus. They were thought to have been captured from the undersides of dead banana leaves (Wilson, 1976). This is likely inasmuch as the I. P. was a banana plantation and Richmond (1893) mentioned that dead leaves hanging from banana plants were investigated because certain bird species frequented these sites for insects.

DISCUSSION

We recognize a total of 119 species of bats overall for northern Central America (Table 1). This constitutes 90% of the 132 Central American species (Jones et al., 1988) and includes eight of the nine regional families of Chiroptera. In northern Central America the insectivorous bats of the families Emballonuridae (11 species), Noctilionidae (two species), Mormoopidae (five species), Natalidae (one species), and Thyropteridae (two species) are Neotropical in affinities; only *Mormoops megalophylla* extends northward into the dry environment of northern México and southwestern United States. The distribution of the large and diverse component of 63 phyllostomid species is primarily Neotropical. Only *Macrotus waterhousii*, among the 23 animalivorous representatives of the Phyllostominae, enters the Nearctic realm. Of the 11 flower-feeding glossophagines, both species of *Leptonycteris* and *Choeronycteris mexicana* extend northward to northern México and southwestern United States. The carolliine (four species) and stenodermatine (22 species) frugivorous bats are Neotropical. The three vampire bats of the subfamily Desmodontinae have extensive Neotropical ranges. The remaining Vespertilionidae and Molossidae, like the Emballonuridae, are insectivorous and have wide distributions. Unlike the emballonurids, and molossids and, especially, the vespertilionids have successfully radiated into truly temperate environments. Consequently, some of the vespertilionids (19 species) and molossids (16 species) of northern Central America have Nearctic affinities. Among the vespertilionids, these are *Myotis auriculus*, *M. californicus*, *M. velifer*, *Pipistrellus subflavus*, *Eptesicus fuscus*, and *Lasiurus intermedius*. The molossids *Eumops glaucinus* and *E. underwoodi* have marginal Nearctic distributions. *Lasiurus blossevillei*, *L. cinereus*, *L. ega*, and *Tadarida brasiliensis* have wide ranges in North and South America that classify them as pan-American.

Ninety-four species are reported for Guatemala. We retain *Macrotis waterhousii* and *Leptonycteris nivalis* in our checklist based on the historical records of Dobson (1876, 1878a). *Myotis cobanensis* tentatively is recognized as an endemic restricted to the Sierra de la Chamá. The southern range limits for six species reach Guatemala (*Balantiopteryx io*, *M. waterhousii*, *L. nivalis*, *Myotis auriculus*, *M. californicus*, and *M. fortidens*). *Balantiopteryx io* is a regional endemic found in southeastern México, Guatemala, and Belize. The distribution of *Lasiurus cinereus* has a marked hiatus. Its range in the Northern Hemisphere apparently terminates in Guatemala, then resumes in South America along the Andean corridor and extends to the southern portion of the continent.

The Honduran checklist presently includes 98 species. The known ranges for *Micronycteris daviesi*, *M. hirsuta*, *M. minuta*, *Tonatia silvicola*, *Carollia castanea*, *Ectophylla alba*, *Myotis riparius*, and *Molossus bondae* reach their reported northern limits inside Honduras. Similarly, the southernmost localities of record for

Table 1.—Distribution of the bats of northern Central America [Guatemala (a), Belize (b), El Salvador (c), Honduras (d), and Nicaragua (e)]. Species that reach their northwesternmost (N) or southeasternmost (S) Central American limits within one of the five countries are indicated. Bats that are endemic (E) to Neotropical México and/or Central America are designated. The distribution of two endemics, *Artibeus inopinatus* and *Myotis cobanensis*, are restricted (R) to northern Central America. Disjunct distributions (D) of certain species appear to end in Central America, only to reappear in South America. Dolan (1989) and Gardner and Ferrell (1990) are followed for the changes in *Molossus* and the use of *Platyrrhinus* in place of *Vampyrops* that differ from Jones et al. (1988).

Species	Gua ^a	Bz ^b	ES ^c	Hon ^d	Nic ^e
Emballonuridae					
<i>Rhynchonycteris naso</i>	X	X	X	X	X
<i>Saccopteryx bilineata</i>	X	X	X	X	X
<i>Saccopteryx leptura</i>	X	X	X	X	X
<i>Cormura brevirostris</i>					N
<i>Peropteryx kappleri</i>	X	X		X	X
<i>Peropteryx macrotis</i>	X	X	X	X	X
<i>Centronycteris maximiliani</i>	X	X		X	
<i>Balantiopteryx io</i> (E)	S	X			X
<i>Balantiopteryx plicata</i> (E)	X		X	X	X
<i>Cyttarops alecto</i>					N
<i>Diclidurus albus</i>	X	X		X	X
Noctilionidae					
<i>Noctilio albiventris</i>	X			X	X
<i>Noctilio leporinus</i>	X	X	X	X	X
Mormoopidae					
<i>Pteronotus davyi</i>	X	X	X	X	X
<i>Pteronotus gymnonotus</i>	X		X	X	X
<i>Pteronotus parnellii</i>	X	X	X	X	X
<i>Pteronotus personatus</i>	X	X	X	X	X
<i>Mormoops megalophylla</i> (D)	X	X	X	S	
Phyllostomidae					
<i>Micronycteris brachyotis</i>	X	X			X
<i>Micronycteris daviesi</i>				N	
<i>Micronycteris hirsuta</i>				N	X
<i>Micronycteris megalotis</i>	X	X	X	X	X
<i>Micronycteris minuta</i>				N	X
<i>Micronycteris nicefori</i>		N			X
<i>Micronycteris schmidtorum</i>	X	X		X	X
<i>Micronycteris sylvestris</i>				X	X
<i>Macrotus waterhousii</i>	S				
<i>Lonchorhina aurita</i>	X	X	X	X	
<i>Macrophyllum macrophyllum</i>	X	X	X	X	X
<i>Tonatia bidens</i>	X	X		X	X
<i>Tonatia brasiliense</i>	X	X		X	X
<i>Tonatia evotis</i> (E)	X	X		S	
<i>Tonatia silvicola</i>				N	X
<i>Mimon cozumelae</i>	X	X		X	
<i>Mimon crenulatum</i>	X	X		X	X
<i>Phyllostomus discolor</i>	X		X	X	X
<i>Phyllostomus hastatus</i>	X	N		X	X
<i>Phylloderma stenops</i>	X	X		X	
<i>Trachops cirrhosus</i>	X	X	X	X	X
<i>Chrotopterus auritus</i>	X	X	X	X	X
<i>Vampyrum spectrum</i>	X	X		X	X
<i>Glossophaga commissarisi</i>	X	X	X	X	X
<i>Glossophaga leachii</i> (E)	X		X	X	X
<i>Glossophaga soricina</i>	X	X	X	X	X

Table 1.—Continued.

Species	Gua ^a	Bz ^b	ES ^c	Hon ^d	Nic ^e
<i>Leptonycteris curasoae</i> (D)	x		x	S	
<i>Leptonycteris nivalis</i>	S				
<i>Lonchophylla robusta</i>					N
<i>Anoura geoffroyi</i>	x		x	x	x
<i>Lichonycteris obscura</i>	x	N		x	x
<i>Hylonycteris underwoodi</i> (E)	x	x			x
<i>Choeroniscus godmani</i>	x		x	x	x
<i>Choeronycteris mexicana</i>	x			S	
<i>Carollia brevicauda</i>	x	x		x	x
<i>Carollia castanea</i>				N	x
<i>Carollia perspicillata</i>	x	x	x	x	x
<i>Carollia subrufa</i> (E)	x		x	x	x
<i>Sturnira ludovici</i>	x		x	x	x
<i>Sturnira lilium</i>	x	x	x	x	x
<i>Vampyressa macconnelli</i>					N
<i>Vampyressa nymphaea</i>					N
<i>Vampyressa pusilla</i>	x	x		x	x
<i>Uroderma bilobatum</i>	x	x	x	x	x
<i>Uroderma magnirostrum</i>	x		x	x	x
<i>Artibeus inopinatus</i> (E,R)			N	x	S
<i>Artibeus intermedius</i>	x	x	x	x	x
<i>Artibeus jamaicensis</i>	x	x	x	x	x
<i>Artibeus lituratus</i>	x	x	x	x	x
<i>Ectophylla alba</i> (E)				N	x
<i>Platyrrhinus helleri</i>	x	x	x	x	x
<i>Vampyrodes caraccioli</i>	x	x		x	x
<i>Chiroderma salvini</i>	x		x	x	
<i>Chiroderma villosum</i>	x	x	x	x	x
<i>Dermanura azteca</i> (E)	x		x	x	
<i>Dermanura phaeotis</i>	x	x	x	x	x
<i>Dermanura tolteca</i>	x	x	x	x	x
<i>Dermanura watsoni</i>	x	x		x	x
<i>Enchisthenes hartii</i>	x		x	x	
<i>Centurio senex</i>	x	x	x	x	x
<i>Desmodus rotundus</i>	x	x	x	x	x
<i>Diaemus youngi</i>			x		x
<i>Diphylla ecaudata</i>	x	x	x	x	x
Natalidae					
<i>Natalus stramineus</i>	x	x	x	x	x
Thyropteridae					
<i>Thyroptera discifera</i> (D)					N
<i>Thyroptera tricolor</i>	x	x		x	
Vespertilionidae					
<i>Myotis albescens</i>	x			x	x
<i>Myotis auriculus</i>	S				
<i>Myotis californicus</i>	S				
<i>Myotis cobanensis</i> (E)	R				
<i>Myotis elegans</i> (E)	x	x		x	x
<i>Myotis fortidens</i>	S				
<i>Myotis keaysi</i>	x	x	x	x	x
<i>Myotis nigricans</i>	x		x	x	x
<i>Myotis riparius</i>				N	x
<i>Myotis velifer</i>	x		x	S	
<i>Pipistrellus subflavus</i>	x			S	
<i>Eptesicus furinalis</i>	x	x		x	x

Table 1.—Continued.

Species	Gua ^a	Bz ^b	ES ^c	Hon ^d	Nic ^e
<i>Eptesicus fuscus</i>	x		x	x	
<i>Lasiurus blossevillii</i>	x	x	x	x	x
<i>Lasiurus cinereus</i> (D)	S				
<i>Lasiurus ega</i>	x	x		x	
<i>Lasiurus intermedius</i>	x	x	x	S	
<i>Rhogeessa tumida</i>	x	x	x	x	x
<i>Bauerus dubiaquercus</i> (E)	x	x		x	
Molossidae					
<i>Molossops greenhalli</i>				x	
<i>Tadarida brasiliensis</i>	x			x	
<i>Nyctinomops laticaudatus</i>	x	x	x	x	
<i>Eumops auripendulus</i>	x	x	x	x	x
<i>Eumops bonariensis</i>		x		x	x
<i>Eumops glaucinus</i>		x		x	x
<i>Eumops hansae</i>				x	
<i>Eumops underwoodi</i>		x	x	x	S
<i>Promops centralis</i>	x			x	x
<i>Molossus aztecus</i>	x			x	x
<i>Molossus bondae</i>				N	x
<i>Molossus coibensis</i>			x		
<i>Molossus molossus</i>	x	x	x	x	x
<i>Molossus pretiosus</i>					N
<i>Molossus rufus</i>	x	x	x	x	x
<i>Molossus sinaloae</i>	x	x		x	x
Totals	119	94	69	98	88

Tonatia evotis, *Choeronycteris mexicana*, *Myotis velifer*, *Pipistrellus subflavus*, and *Lasiurus intermedius* are Honduran. *Tonatia evotis* is a regional endemic. *Mormoops megalophylla* and *Leptonycteris curasoae* have disjunct distributions that appear to terminate in Olancho and the Pacific lowlands of Honduras, but these species also occur in northern South America.

The literature for Nicaragua documents 88 species of bats including *Cormura brevirostris*, *Cyttarops alecto*, *Lonchophylla robusta*, *Vampyressa macconnelli*, *V. nymphaea*, and *Molossus pretiosus*, which have not been recorded farther north. While these tropical species occur in Nicaragua, the temperate vespertilionid assemblage listed for Guatemala and Honduras is noticeably absent. Also missing from Nicaragua are bats (e.g., *Chiroderma salvini*, *Dermanura azteca*, *E. hartii*, *Eptesicus fuscus*, and *Lasiurus cinereus*) that inhabit higher elevations. This faunal variation reflects the low mountains in northern Nicaragua, which farther south become the lower topographic relief of the Nicaraguan depression. The latter forms a transitional area between the northern Central American block and the remainder of the isthmus. The ranges of *Artibeus inopinatus* and *Eumops underwoodi* reach southeastern limits in Nicaragua. The former is a restricted endemic of the Pacific lowlands of El Salvador, Honduras, and Nicaragua. *Thyroptera discifera* is known in Central America only from one locality in the Caribbean lowlands of Nicaragua, although it also occurs in northern South America.

The occurrence of some species in northern Central America appears to be primarily at elevations above 500 m. These bats include *Leptonycteris nivalis*, *Choeronycteris mexicana*, *Chiroderma salvini*, *Dermanura azteca*, *D. tolteca*, *Enchisthenes hartii*, *Myotis auriculus*, *M. californicus*, *M. cobanensis*, *M. velifer*,

Eptesicus fuscus, *Lasiurus cinereus*, *Tadarida brasiliensis*, and *Molossus aztecus*. Noticeably unreported from the mountains of northern Central America is *Eptesicus brasiliensis*, a pronounced hiatus between known localities in Chiapas and Costa Rica (Hall, 1981). The montane species *Sturnira mordax* is endemic to Costa Rica and western Panamá (Olmos and de Sousa, 1989) and not known northward. The name *ludovici* Anthony, 1924, has been applied to the remaining larger *Sturnira* of montane Middle America (de la Torre, 1961). We concur with Timm et al. (1989) that these fruit bats will probably prove to represent a composite of species and that true *S. ludovici* is an Andean endemic. Consequently, Goodwin's (1940) name *S. hondurensis* would be available for these bats in northern Central America.

Patterns of occurrence at lower elevations for some species reflect a preference for specific climatic conditions. The distributions of *Balantiopteryx plicata*, *Glossophaga leachii*, *Carollia subrufa*, *Uroderma magnirostrum*, *Artibeus inopinatus*, and *Molossus coibensis* in northern Central America are restricted to drier environments associated with the Pacific slope and dry intermontane valleys. The moisture gradient along the Caribbean and Gulf versants identifies the restricted distributions of *Centronycteris*, *Cyttarops*, *Micronycteris daviesi*, *M. nicefori*, *Tonatia bidens*, *T. evotis*, *Mimon cozumelae*, *M. crenulatum*, *Lonchophylla robusta*, *Hylonycteris*, *Carollia castanea*, *Vampyroides*, *Vampyressa nymphaea*, *V. pusilla*, *Ectophylla*, *Dermanura watsoni*, *Thyroptera discifera*, *Myotis albescens*, *M. riparius*, *Pipistrellus*, *Bauerus*, and *Molossus bondae*.

The bat faunas of the coastal countries of El Salvador (58) and Belize (69) are characterized by species indicative of the dry Pacific coastal region in the former and wet Caribbean lowlands of the latter. The limited montane habitats in El Salvador support additional species such as *Sturnira ludovici*, *Dermanura azteca*, *Enchisthenes hartii*, and *Myotis velifer*, which increase species composition. Upland regions in Belize are not as elevated and the known fauna lacks montane species and is limited to *Dermanura tolteca*, a species of intermediate elevation. The northernmost neotropical localities for *Micronycteris nicefori*, *Phyllostomus hastatus*, and *Lichonycteris obscura* are in southern Belize.

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GAZETTEER

Localities mentioned in the text from Guatemala, Belize, El Salvador, Honduras, Nicaragua, and Costa Rica are listed alphabetically under departments, districts, or provinces. The number for each locality corresponds with the number on the accompanying map (Fig. 1).

GUATEMALA

Alta Verapaz

- 1) Cahabón 15°34'N/89°49'W
- 2) Cobán 15°29'N/90°19'W

Baja Verapaz

- 3) Purulhá 15°16'N/90°12'W
- 4) Salamá 15°06'N/90°16'W
- 5) San Jerónimo 15°03'N/90°12'W

Chimaltenango

- 6) San Pedro Yepocapa 14°30'N/90°57'W

El Petén

- 7) Flores 16°56'N/89°53'W
- 8) La Libertad 14°37'N/91°42'W
- 9) Poptún 16°21'N/89°26'W
- 10) Parque Nacional Tikal 17°20'N/89°39'W

El Progreso

- 11) El Progreso 14°51'N/90°04'W

Escuintla

- 12) Puerto de San José 13°55'N/90°49'W

Guatemala

- 13) Amatítlan 14°29'N/90°37'W
- 14) Guatemala 14°38'N/90°31'W

Huehuetenango

- 15) Aguacatán 15°21'N/91°18'W

Izabal

- 16) El Estor 15°32'N/89°21'W
- 17) Santo Tomás de Castilla 15°42'N/88°37'W

Quiché

- 18) Sacapulas 15°20'N/91°04'W

Sacatepéquez

- 19) Antigua Guatemala 14°34'N/90°44'W
- 20) Ciudad Vieja 14°31'N/90°46'W
- 21) San Miguel Dueñas 14°31'N/90°48'W

Santa Rosa

- 22) Chiquimulilla 14°05'N/90°23'W

Sololá

- 23) Panajachel 14°44'N/91°09'W

Zacapa

- 24) Santa Cruz 15°01'N/89°39'W

Unspecified locality

- 25) "Volcán de Fuego" 14°29'N/90°53'W

BELIZE

Belize

- 26) Half-Moon Caye 17°12'N/87°32'W

Cayo

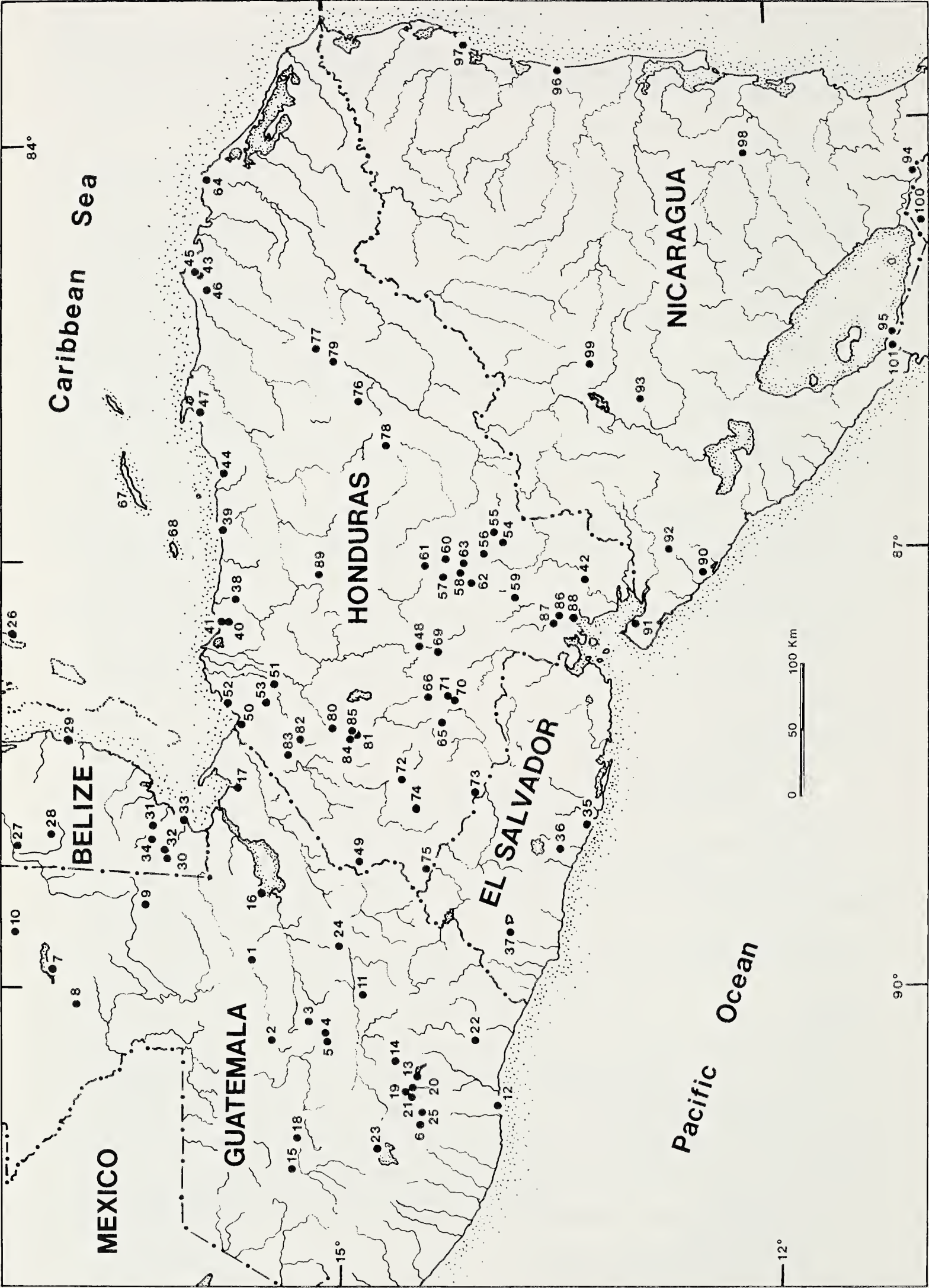
- 27) Central Farm, Baking Pot 17°11'N/89°00'W
- 28) Mountain Pine Ridge 16°53'N/88°55'W

Stann Creek

- 29) Sittee (=Freetown) 16°50'N/88°17'W

Toledo

- 30) Aguacate 16°10'N/89°06'W
- 31) Big Falls 16°19'N/88°51'W
- 32) Blue Creek 16°12'N/89°03'W
- 33) Orange Point 16°04'N/88°49'W
- 34) Salamanca (Forestry Camp) 16°16'N/89°01'W



EL SALVADOR

La Paz

35) La Herradura 13°21'N/88°58'W

36) San Luis Talpa 13°29'N/89°06'W

Sonsonate

37) Volcán Izalco 13°49'N/89°38'W

HONDURAS

Atlántida

38) Jilamo 15°35'N/87°21'W

39) La Ceiba 15°47'N/86°50'W

40) Lancetilla 15°42'N/87°28'W

41) Tela 15°43'N/87°29'W

Choluteca

42) Choluteca 13°08'N/87°12'W

Colón

43) Aguacates 15°55'N/85°04'W

44) Balfate 15°48'N/86°25'W

45) Laguna Bacalar 15°57'N/85°01'W

46) Sico 15°50'N/85°10'W

47) Trujillo 15°55'N/86°00'W

Comayagua

48) Comayagua 14°25'N/87°38'W

Copán

49) Copán 14°50'N/89°09'W

Cortés

50) Cuyamel 15°38'N/88°12'W

51) La Lima 15°24'N/87°56'W

52) Omoa 15°43'N/88°02'W

53) San Pedro Sula 15°28'N/88°01'W

El Paraíso

54) Guinope 13°51'N/86°55'W

55) Yuscarán 13°56'N/86°52'W

Francisco Morazán

56) El Zamorano 14°00'N/87°02'W

57) La Flor Archaga 14°17'N/87°11'W

58) El Rosario, Parque Nacional La Tigra 14°13'N/87°05'W

59) Sabana Grande 13°50'N/87°15'W

60) San Juan de Flores 14°15'N/87°02'W

61) Talanga 14°28'N/87°06'W

62) Tegucigalpa 14°04'N/87°13'W

63) Valle de Angeles 14°09'N/87°03'W

Gracias a Dios

64) Río Patuca 15°50'N/84°17'W

Intibucá

65) La Esperanza 14°16'N/88°10'W

66) Quiraguira 14°22'N/87°55'W

Islas de la Bahía

67) Isla de Roatán 16°23'N/86°30'W

68) Isla de Utila 16°06'N/86°56'W

La Paz

69) La Paz 14°16'N/87°40'W

70) Muye 14°09'N/87°55'W

71) San José 14°13'N/87°56'W

Lempira

72) Gracias 14°35'N/88°35'W

73) La Virtud 14°02'N/88°35'W

←

Fig. 1.—Distribution of localities in Guatemala, Belize, El Salvador, Honduras, Nicaragua, and northern Costa Rica. The numbers refer to those listed in the gazetteer.

Ocotepeque	
74) Belén Gualcho	14°29'N/88°47'W
75) Nueva Ocotepeque	14°26'N/89°11'W
Olancho	
76) Catacamas	14°53'N/85°55'W
77) Dulce Nombre de Culmi	15°09'N/85°37'W
78) Juticalpa	14°42'N/86°15'W
79) San José, Río Tinto	14°59'N/85°46'W
Santa Bárbara	
80) Ilama	15°04'N/88°13'W
81) Macholola	14°52'N/88°16'W
82) Petoa	15°15'N/88°18'W
83) Quimistán	15°20'N/88°23'W
84) San Nicolás	14°54'N/88°19'W
85) Santa Bárbara	14°53'N/88°14'W
Valle	
86) Jicaro Galán	13°31'N/87°28'W
87) Nacaome	13°31'N/87°30'W
88) San Lorenzo	13°25'N/87°27'W
Yoro	
89) Yoro	15°09'N/87°07'W
NICARAGUA	
Chinandega	
90) El Realejo	12°32'N/87°10'W
91) Potosí	13°01'N/87°30'W
92) "Volcán de Casita"	12°42'N/86°58'W
Matagalpa	
93) Matagalpa	12°55'N/85°55'W
Río San Juan	
94) El Castillo	11°01'N/84°24'W
Rivas	
95) Cárdenas	11°12'N/85°31'W
Zelaya Norte	
96) Prinzapolka	13°24'N/83°34'W
97) Puerto Cabezas	14°02'N/83°23'W
Zelaya Sur	
98) Rama	12°09'N/84°15'W
Unspecified locality	
99) "Peña Blanca"	12°41'N/85°41'W
COSTA RICA	
Alajuela	
100) San Emilio	10°57'N/84°44'W
Guanacaste	
101) Peñas Blancas	11°13'N/85°38'W

ADDENDUM

Recent karyotypic data (Audet et al., 1993) confirmed the presence of a species distinct from *Rhogeessa tumida* in the Yucatan Peninsula region including northern Belize and Guatemala. The available name of *Rhogeessa aeneus* Goodwin, 1958 was assigned and is added to the bat faunal lists of Belize and Guatemala. The generic variability within the *R. tumida* "complex" over its entire range remains incompletely defined.

AUDET, D., M. D. ENGSTROM, AND M. B. FENTON. 1993. Morphology, karyology, and echolocation calls of *Rhogeessa* (Chiroptera: Vespertilionidae) from the Yucatan Peninsula. *Journal of Mammalogy*, 74(2):498–502.

FOSSIL PENAEIDAE (CRUSTACEA: DECAPODA) FROM THE
LOYOLA FORMATION, ECUADORRODNEY M. FELDMANN¹

Research Associate, Section of Invertebrate Paleontology

LUIS CHIRINO-GALVEZ¹GREGORY L. MASON¹JESSICA L. ANDERSON¹PATRICK W. DUNCAN¹REBECCA A. WARD¹DAVE R. SALEM¹

ABSTRACT

Specimens of fossil shrimp, preserved in the fine clastic sediments of the middle Miocene Loyola Formation, within the Cuenca Basin, Ecuador, have been identified as *?Penaeus maddenii* n. sp. Their presence strongly suggests that marine conditions existed within the basin during the deposition of some of the Loyola Formation and that the geological history of marine influence in Andean intermontane basins is complex. This observation is reinforced by the presence of claws of a crab identified as *?Necronectes proavitus* (Rathbun) from a nearby locality within the formation. Because the identification of the crab claws is questionable, their use as a stratigraphic index is more limited than previously suggested.

INTRODUCTION

The Loyola Formation consists of about 500 m of dominantly thin-bedded shale deposited during the middle Miocene in the Cuenca Basin of Ecuador. The unit is significant in that it contains a diverse assemblage of vertebrate, invertebrate, and plant fossils. Among these are numerous casts of penaeid shrimp that were apparently deposited in one or two brief events. The Loyola Formation is also significant in that analysis of its sediments and enclosed fossils can provide information on the geologic history of the Cuenca Basin. Depth, temperature, and salinity conditions within the basin at the time of deposition of the fossil shrimp can be deduced by analyzing the enclosing sediment using thin sections, SEM, and X-ray analysis in conjunction with interpretation of fossil material. The primary purpose of this paper is to describe the fossil shrimp remains and to present some observations on their implications for the geologic history of the Cuenca Basin.

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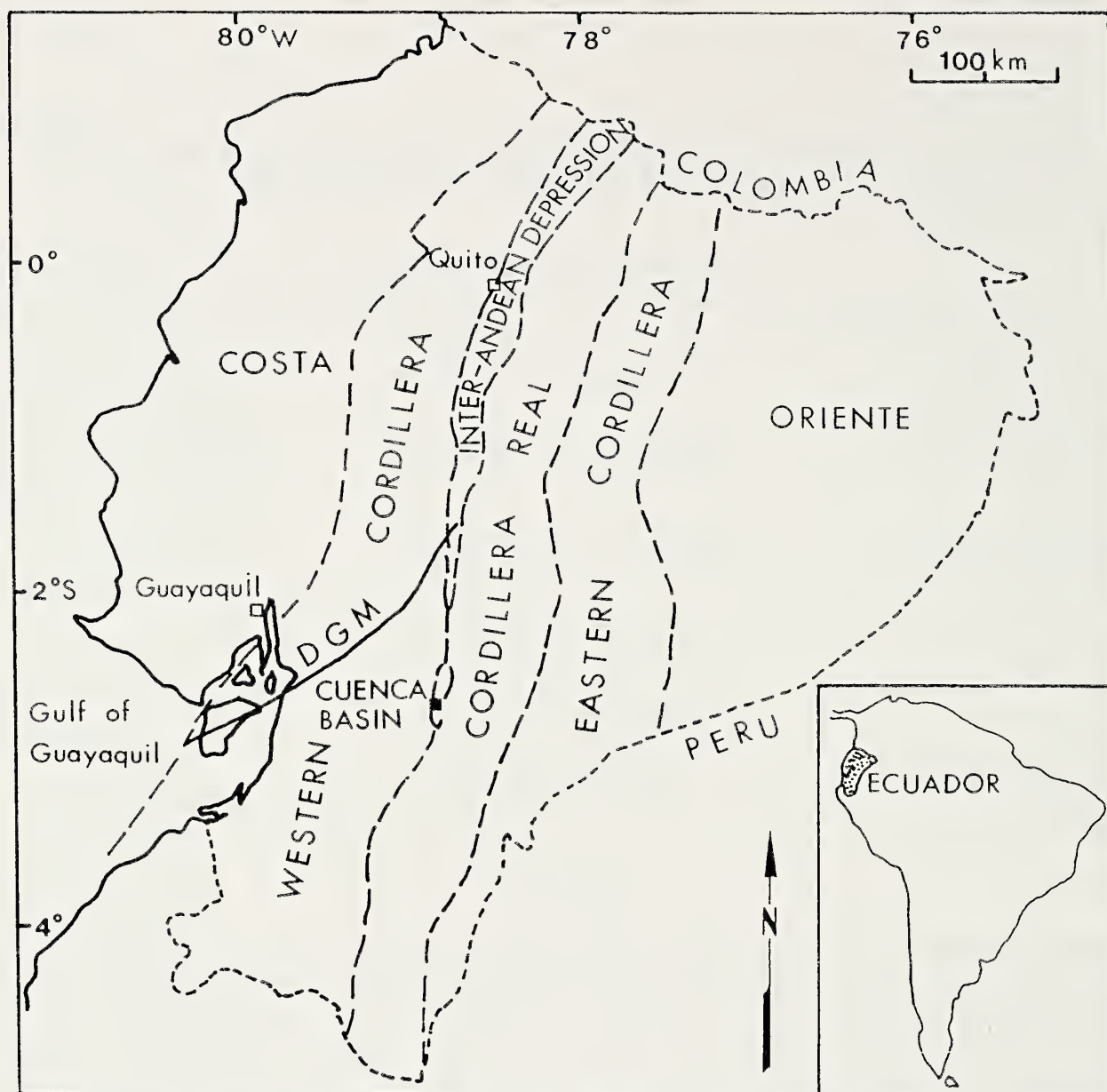


Fig. 1.—Generalized map of Ecuador showing the major tectonic regions referred to in the text (modified from Baldock, 1985). The southern trace of the Dolores-Guayaquil megashear (DGM) is superimposed from Megard (1989). Fossil shrimp were collected from the Cuenca Basin and the black square indicates the location of the larger scale geologic location map, Fig. 2.

REGIONAL SETTING

In no place are the northern Andes narrower than in central-southern Ecuador, the Sierra, where the average width is 100–140 km. North of latitude $2^{\circ}15'S$ the Andes are divided into two parallel ranges, the Cordillera Real and Eastern Cordillera to the east with peaks exceeding 4500 m, and a Western Cordillera separated by a continuous inter-Andean valley and the Cauca-Patia graben. South of latitude $2^{\circ}15'S$ the Sierra is more uniformly mountainous, with few peaks exceeding 4000 m. The Cuenca intermontane basin, lying within this region, is of Miocene age, and has been described as a strike-slip basin (Lavenu and Noblet, 1989; Fig. 1).

The northern Andes are a cordilleran orogen, whose western parts consist of accreted terrains of oceanic origin (Megard, 1989). The boundary (suture) between oceanic and continental crust is the Dolores-Guayaquil Megashear (DGM) (Fig. 1). The DGM follows approximately the Cauca-Patia graben and the inter-Andean valley in the north and bends southwest at approximately latitude $2^{\circ}S$ into the Gulf of Guayaquil and ends at a triple point in the Ecuadorian trench. To the east of the DGM suture is silicic crust of continental origin.

The Andean orogenic cycle began in Norian times, when the sea invaded extensive continental areas (Megard, 1989). In Lower Cretaceous times, under the influence of the great worldwide transgression, the Oriente of Ecuador, situated on what then constituted the western edge of the South American plate, became submerged to form a broad continental shelf which persisted through Santonian time (Feininger and Bristow, 1980).

The massif of the Proto-Cordillera Real of Colombia began to emerge during the early Tertiary, which was a period of deformation and/or uplift known as the Incaic phase of the Andean orogeny. In western Colombia and Ecuador, during the late Eocene to early Oligocene, diastrophism correlating with the Andean orogenic cycle affected the Sierra. This resulted in local folding, low-grade metamorphism and widespread plutonism (Baldock, 1985). Uplift and minor overthrusting along the Sub-Andean fault zone contributed to the rise of the Proto-Andes and the formation of intermontane basins, mostly of Miocene age. These include the Cuenca Basin of Ecuador.

Important changes occurred in western Colombia and Ecuador in Eocene time with the development of a sedimentary basin, the Bolivar Geosyncline of Harrington (1962). This basin was interposed between the rising Cordilleras and a foundered landmass to the west. The basin extended from the Gulf of Guayaquil northwards through Colombia and into the Caribbean. Marine sedimentation began in the south in the early to middle Eocene, gradually encroached northward and continued intermittently into the upper Miocene (Nygren, 1950). The Gulf of Guayaquil, "the Ecuadorian portal" or "Guayaquil portal" to this basin, is a transverse basin that forms a divide in the present drainage system and represents a deep portion of the major basin, the "Bolivar Geosyncline." The entire basin periodically served as a seaway during various times from Eocene to late Pliocene (Nygren, 1950).

In early Oligocene time the sea advanced through the Ecuadorian portal and reached the Oriente of Ecuador (Harrington, 1962). The upper Oligocene sea spread over great areas, extending as far east as the Cauca-Patia graben and throughout the length of the geosyncline with very low borderlands on the east and the west (Nygren, 1950). This seaway persisted, with continued shallowing, up to the lower middle Miocene.

During the upper middle Miocene, widespread volcanism occurred throughout the southern and central Andes (Hall and Calle, 1982). Increased orogenic movement was accompanied by faulting and igneous activity. The western border of the basin was down faulted beneath the Pacific and the eastern borderland raised into the high peaks of the Western Cordillera. The sea was then forced out, except in the deepest areas and the gulfs at each end (Nygren, 1950).

The area of the Gulf of Guayaquil apparently was more mobile than areas to the north and south. This mobility resulted in the opening of the Gulf, which probably began in the late Eocene. The Gulf of Guayaquil is a pull-apart basin resulting from the northward motion of the Western Ecuadorian Columbian Megablock along major longitudinal fault zones, like the DGM (Megard, 1989). During the pull-apart events many deep basins were formed which can be interpreted as fault blocks that were left behind.

During the Miocene, sediments were deposited within the intermontane basins in the progressively uplifted cordillera. Plutonism was widespread along the Western Cordillera. In the late Miocene, arching of the uplifted Sierra reintroduced a tensional regime that caused the development of the inter-Andean valley, bounded by reactivated normal faults.

The pull-apart of the Gulf of Guayaquil resulted in subsidence of the fault blocks that remained and creation of deep marine basins less than 75 km west of Cuenca. The area of the Cuenca Basin is bounded by many faults trending in a southwest to northeast direction. Reactivation of these faults during the Quenca 3 phase of the Andean orogeny may have resulted in subsidence of both the low Western Cordillera and the inter-Andean valleys, which were also being overthrust from the east by the Eastern Cordillera. The lower to upper Miocene age of the Loyola Formation, which was deposited in the Cuenca Basin, corresponds to the pull-apart of the Gulf of Guayaquil, marine invasion of the "Bolivar Geosyncline," and a global eustatic rise in sea-level estimated at 150 m (Hardenbol et al., 1982).

STRATIGRAPHY AND LITHOLOGY

There are seven recognized sedimentary formations within the Cuenca Basin (Fig. 2, 3). The oldest of these is Cretaceous in age. The basal relationship of the Cretaceous Yunguilla Formation is unknown (Bristow, 1973). The Miocene Biblián Formation is suspected to unconformably overlie the Cretaceous Yunguilla Formation supporting a depositional hiatus between the Cretaceous and the Miocene. In the depositional center of the basin, the basal contact of the Biblián Formation has not been explored to confirm this hiatus.

The Miocene Loyola Formation conformably overlies the Miocene Biblián Formation in the center of the basin and is exposed along the flanks of the Biblián Anticline and the Azogues Syncline. Toward the northeast margin of the basin, the Loyola Formation oversteps the Biblián to lie directly on the Yunguilla Formation. This may suggest a low stand of basin water allowing erosion along the shorelines prior to transgression and deposition of the basal beds, including the conglomerates, of the Loyola Formation. The fine-grained nature of the succeeding beds in the formation represents a period of maximum extent of the Cuenca Basin during the Miocene (Noblet and Marocco, 1989). This was a period of greatest likelihood for marine transgression into the basin prior to its closure.

The Loyola Formation consists largely of fissile gray to cream shales and silty shales with a conglomeratic unit at the base. Limestone lenses occur throughout, as do gypsum veins and coatings on joints and bedding planes (Bristow and Parodiz, 1982). Small beds (2–3 cm) of calcareous sandstones have been noted in the basal beds (Bristow, 1973). The thickness of the Loyola Formation has been estimated at 360 m, with the basal conglomerates comprising up to 45 m locally (Bristow, 1973). The basal conglomerates are well developed to the northeast, and appear to die out toward the center and southwest of the basin.

Other than fish remains and leaves, fossils are uncommon outside of the basal beds. The basal beds are, however, the most richly fossiliferous beds within the Cuenca Basin and have yielded 26 of the 33 species of bivalves and gastropods identified by Bristow and Parodiz (1982). Ostracods and molluscs occur in the basal sequence, with local shell beds composed almost entirely of *Doryssa bibliana* (Mollusca: Gastropoda) (Bristow and Parodiz, 1982). Echinoids have also been reported from the basal beds of the Loyola (Erazo Vallejo, 1965); but the whereabouts of the documenting specimens is not known and their presence has not been confirmed. Crustacean material, tentatively identified as *Necronectes proavitus* (Rathbun), is reported to be common in the basal sequence (Bristow and Parodiz, 1982). Thus, the fossils which have been identified previously from the basal beds would seem to indicate at least an initial marine condition during deposition of the Loyola Formation.

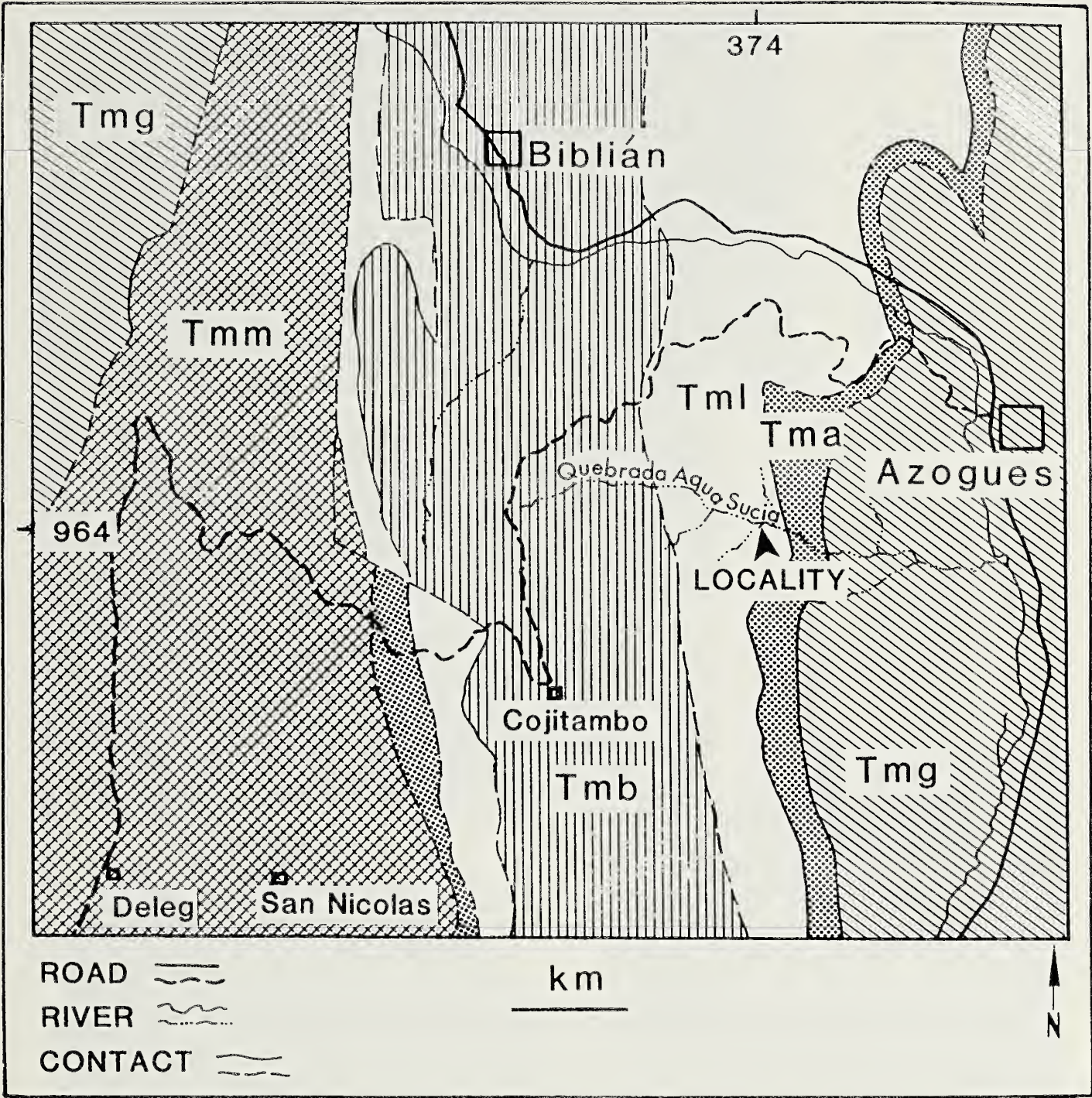


Fig. 2.—Geologic map of the region surrounding Azogues, Ecuador, from which *?Penaeus madden* n. sp. was collected. Tmb = Biblián Formation; Tml = Loyola Formation; Tma = Azogues Formation; Tmg = Guapán Formation; Tmm = Mangán Formation. Base map taken from the Azogues (1:50,000) quadrangle from the geologic map of Ecuador and provided by Dr. Richard Madden.

SYSTEMATIC PALEONTOLOGY

- Order Decapoda Latreille, 1803
- Infraorder Penaeidea de Haan, 1849
- Superfamily Penaeoidea Rafinesque, 1815
- Family Penaeidae Rafinesque, 1815
- Genus *Penaeus* Fabricius, 1798
- ?Penaeus madden* new species
- (Fig. 4, 5)

Diagnosis.—Very small penaeid with extremely thin cuticle, long rostrum with dorsal and, apparently, ventral spines; distinguished from other members of the genus by having relatively well-developed cervical groove, antennular flagellae

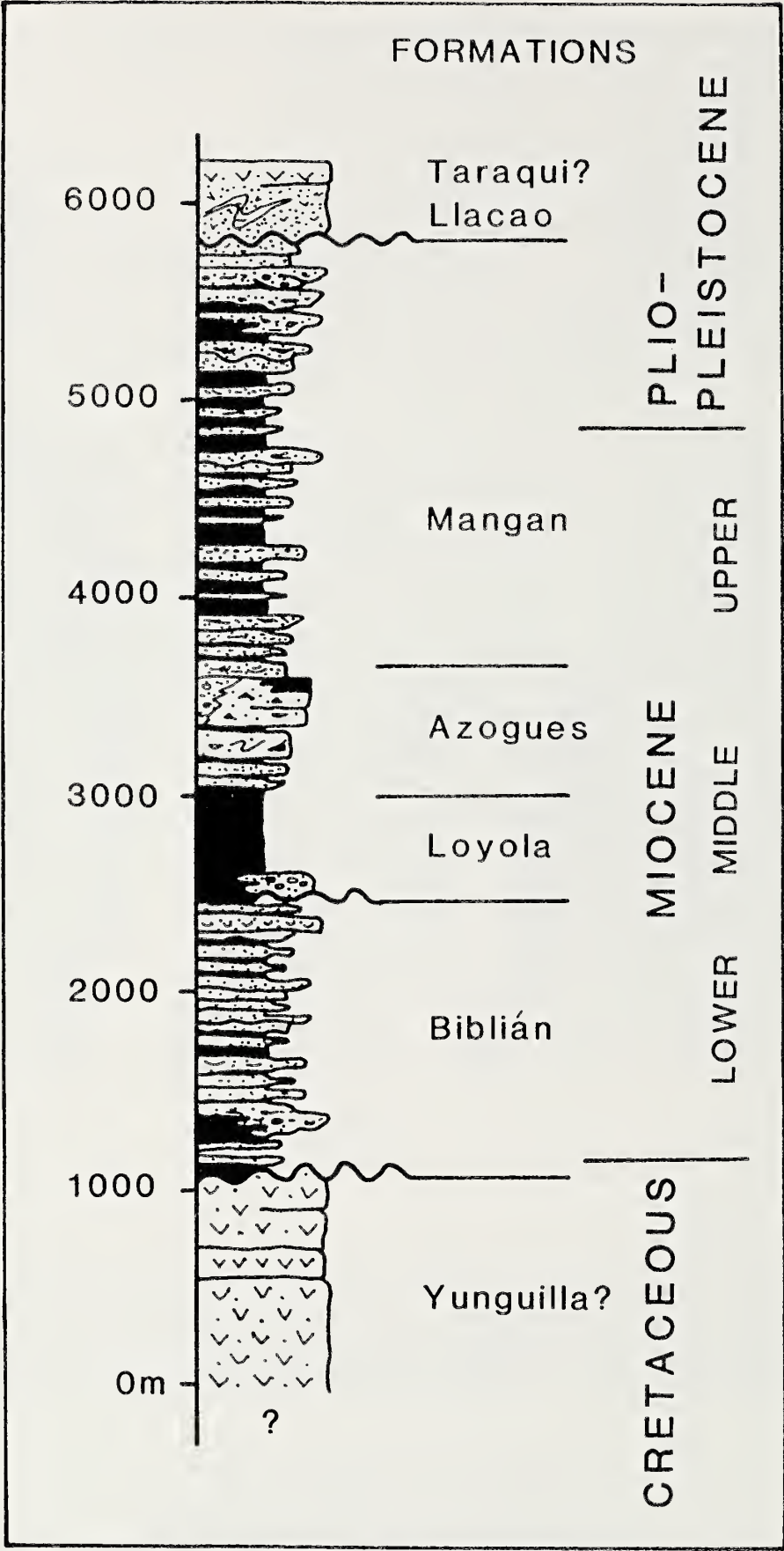
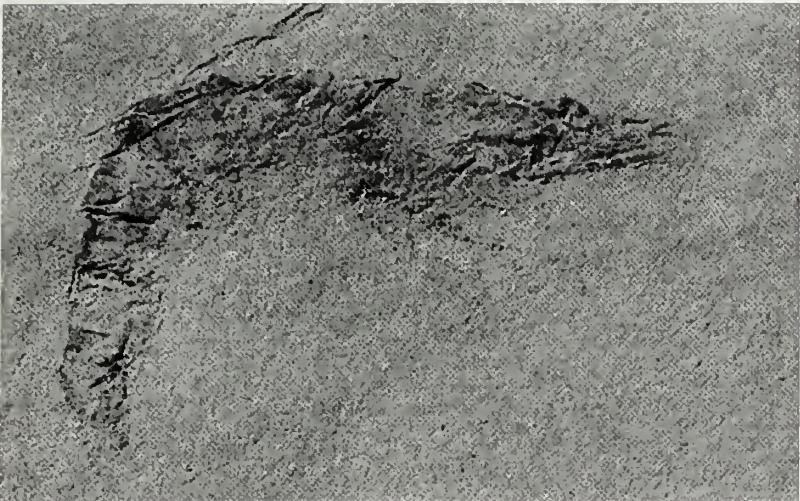


Fig. 3.—Stratigraphic section of rocks in the Cuenca Basin showing the distribution of coarse and fine clastic rocks in the Tertiary sequence (modified from Noblet and Marocco, 1989). Note that the Azogues and Guapán formations, as denoted on Fig. 2, are considered a single unit, the Azogues Formation, on this section.

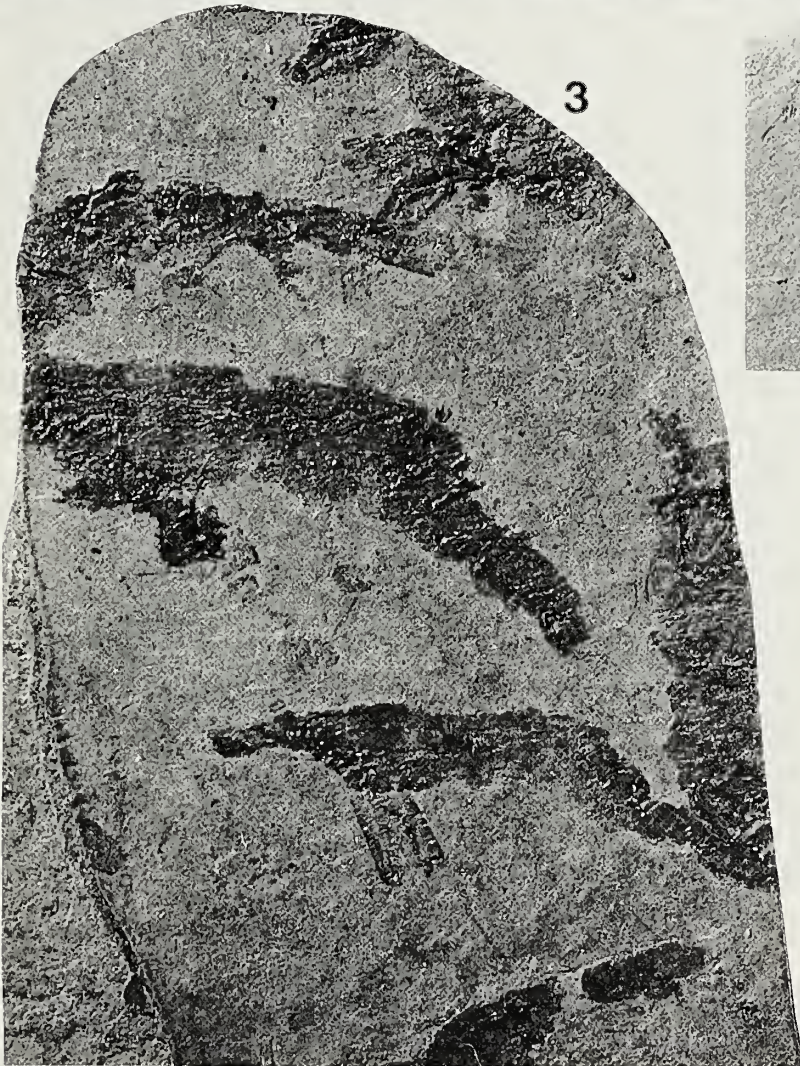
Fig. 4.—?*Penaeus madden*i n. sp. 1, Left lateral view of holotype, CM 35820, showing the impression of the antennae and rostrum. 2, Right lateral view of paratype, CM 35821. 3, Six individuals, CM 35822, preserved on a bedding plane. Note the telson and uropods on the uppermost specimen. 4, Left lateral view of incomplete paratype, CM 35823, showing nature of thoracic appendages and detail of abdominal somites. 5, Right lateral view of paratype, CM 35824. Scale bar equals 1 cm.



1



2



3



4



5



longer than carapace; strongly reflexed abdomen with triangular pleurae on somites 1–5 and no overlap of pleuron 2 over that of 1 and 3.

Description.—Cephalothorax longer than high, smooth, apparently lacking spines in orbital region; rostrum about 70% length of carapace measured from base of orbit to posterior margin, uniformly tapering anteriorly, with at least three delicate spines along dorsum and indication of spines on venter, dorsal crest extending posteriorly to cervical groove; orbit small, well defined, eyes and eyestalks relatively short, extending to midlength of rostrum; cervical groove weakly expressed, crossing midline and extending ventrally approximately to level of base of orbit.

Abdomen smooth, uniformly tapering posteriorly, strongly reflexed around somites 2 and 3; abdominal somites 1–3 about equal in length and longer than somites 4–6; pleura of somites 1–5 triangular with ventrally directed, pointed terminations; pleuron of somite 2 not enlarged and not overlapping pleura 1 or 3. Telson tapering distally in lateral view to sharp termination.

Appendages poorly preserved. Antennal scales tapering distally, about as long as rostrum. Antennal flagellae at least four times length of carapace. Antennular flagellae nearly two times length of carapace. Thoracopods elongate, very slender, carried with meri directed anteriorly and distal elements curved downward and posteriorly. Abdominal appendages appear to be flattened and about as long as abdominal somites are high.

Measurements.—Accurate measurements of individual elements of the fossils cannot be made because crushing and distortion make it difficult to identify specific points of reference. Overall lengths of specimens vary from about 14 to 24 mm.

Types.—The holotype, CM 35820, and paratypes, CM 35821–35834, are deposited in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania. Additional paratypes are deposited in the Geology Department, Escuela Politécnica Nacional (EPN), Quito, Ecuador.

Etymology.—The trivial name recognizes Dr. Richard Madden, Department of Biological Anthropology and Anatomy, Duke University Medical Center, Durham, North Carolina, for having collected the material and for making it available to the senior author.

Locality and stratigraphic position.—The specimens were collected from the Loyola Formation on the western flank of the Biblián Anticline in an intermittent stream bed called Quebrada Agua Sucia, locality DU-EPN(Q)-006, Grid reference 374964 on CT-ÑV-E1, Azogues (1:50,000) topographic quadrangle (Fig. 2). Their precise stratigraphic position is uncertain at this time.

Remarks.—The specimens forming the basis for description of this new species exhibit sufficient detail to confirm placement within the Penaeidae and suggest reference to *Penaeus*. The possession of an elongate, serrate rostrum, a generally smooth carapace and abdomen, and recurved abdomen, along with the lack of an enlarged, overlapping pleuron on the second abdominal somite define the familial placement. Although numerous fragments of legs are preserved, the placement and number of chelae cannot be determined.

The pleura tend to be well developed and are triangular which is typical of species of *Penaeus*. Poor preservation of the rostrum does not permit conclusive determination of whether or not the ventral margin of the rostrum is denticulate; however, the holotype has a well-developed rostrum with what appears to be at least one ventral spine. In this regard, the specimens more closely resemble *Penaeus* than they do *Trachypenaeus* Alcock, another genus common to modern waters of the west coast of South America (Méndez, 1981). General morphology

←

Fig. 5.—Bedding plane exposing 12 specimens of ?*Penaeus maddeni* n. sp. showing the nature of the preservation of most of the specimens and the density of specimens on the fossiliferous surfaces, CM 35825. Scale bar equals 1 cm.

of the specimens is most like that of other members of the genus *Penaeus*. Dall et al. (1990:61) observed that "all of the genera [of Penaeidae] have a distinctive appearance or facies, which is difficult to describe, but may be readily recognized with practice." There does not appear to have been any strong ornamentation on the carapace and there are no unusual features such as enlarged or recurved rostral crests or extremely pitted, setose surfaces.

In general, the quality of preservation of fossil penaeids tends to be poor and there are few examples of the group, relative to groups characterized by more strongly calcified skeletons. Thus, it is difficult to make detailed comparisons with other species. The relatively long antennular flagellae, delicate rostrum, and moderately well-developed cervical groove may be taken as important points to distinguish this species from other members of the genus. Measurement of the absolute length of antennular flagellae is difficult, owing to the fact that the elements are broken and disarticulated; but there is no doubt that the flagellae exceed the carapace length. It is possible that the characters of antennular length, form of rostrum, and development of cervical groove are sufficiently important to warrant naming a new genus. However, the quality of the specimens is so poor that this action would be unwise.

The integument of these shrimps is extremely thin, and preservation has resulted in compression and severe wrinkling of the remains. Nonetheless, most of the specimens are preserved as whole animals so that it is probable that the fossils represent dead animals rather than molts. This observation, coupled with the observation that the fossils occur in large numbers, one specimen often overlapping another, on just one or two bedding planes, strongly suggest that all the individuals died and were preserved in a single event. Because shrimp regularly exhibit swarming behavior, the preservation of a large number of individuals cannot be taken as clear evidence of a mass mortality event.

The individuals are small by comparison with other adult representatives of *Penaeus*. Females of most extant species attain total lengths of more than 20 cm (Dall et al., 1990). Thus, it is possible that these fossils represent juveniles, rather than adults.

It is important to note that penaeids are confined largely to marine conditions (Glaessner, 1969:R426); however, most species exhibit juvenile development in estuarine conditions (Dall et al., 1990). The taxa most closely related to the penaeids which have fresh-water representatives are the Atyidae and the Palaemonidae. These families are members of the Caridea and are characterized by having a large pleural flap on the second abdominal somite which overlaps the pleura of the first and third somite. That is not the case in *?Penaeus maddenii*. Thus, the presence of this genus in the Loyola Formation argues strongly for deposition of at least part of the formation under marine or estuarine conditions.

Infraorder Brachyura Latreille, 1803
Superfamily Portunoidea Rafinesque, 1815
Family Portunidae Rafinesque, 1815
Genus *Necronectes* A. Milne Edwards, 1881
?Necronectes proavitus (Rathbun), 1918
(Fig. 6)

Remarks. — *Necronectes proavitus* was initially reported from the Loyola Formation by Bristow (1973) and that observation was republished by Bristow and Parodiz (1982). The species was neither described nor illustrated, but simply was included in a list of taxa collected from the unit. However, the species has special

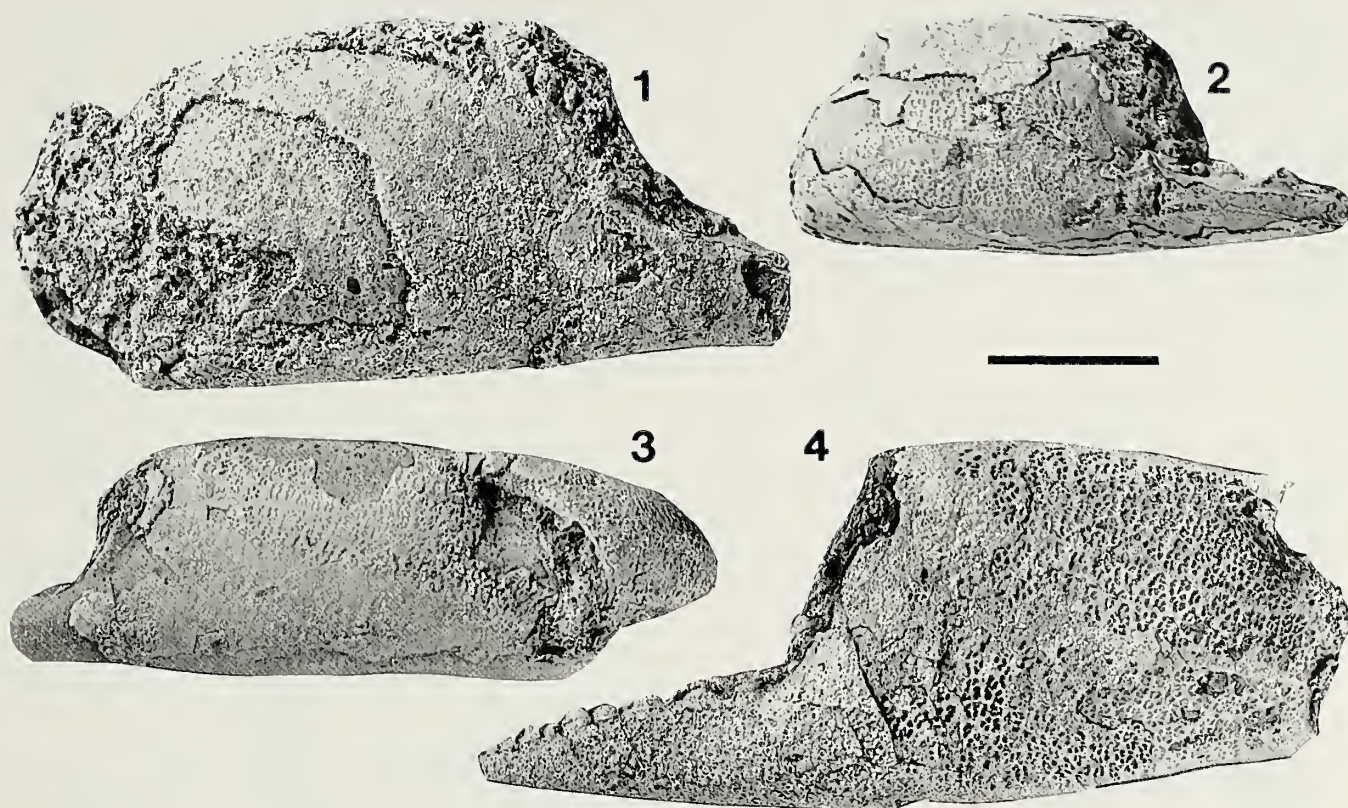


Fig. 6.—?*Necronectes proavitus* (Rathbun). 1, Outer surface of right cheliped, BMNH IN 61453. 2, Outer surface of right cheliped, BMNH IN 61454. 3, Outer surface of left cheliped, with attached carpus, BMNH IN 61455. 4, Outer surface of left cheliped, BMNH IN 61456. Scale bar equals 1 cm.

significance because it provided the best independent, paleontological evidence for the middle Miocene age of the Loyola Formation (Bristow and Parodiz, 1982: 11). In the original notice of the species, the identification was given as "... a form close to *Necronectes proavitus* (Rathbun) known only from the Miocene of Gatun" (Bristow, 1973:23). Thus, the establishment of the age of the Loyola Formation, based upon this species would have to be considered questionable. The subsequent reference to the species as an index to the middle Miocene (Bristow and Parodiz, 1982:11) gave no indication of the equivocal nature of the identification.

The material basis for this determination is 21 bits of claw material, including ten moderately complete hands and 11 fragments of carpi, fingers, and hands originally identified by S. F. Morris and now deposited in The Natural History Museum, London, under catalogue numbers BMNH IN 61453–61462. The material was collected from a single locality (Grid reference 404947) near the village of Antonio Borrero (also known as Charasol) (Bristow, 1973), about 5.5 km southeast from the locality at which the shrimp were collected. Re-examination of that material confirms that the specimens likely belong to a portunid or xanthid crab and that they are similar to those preserved on the holotype (Rathbun, 1918: pls. 55, 56) of *Gatunia proavita* Rathbun. However, firm identification of this species, based solely upon fragmentary claws, is not possible, so that although the specimens may be conspecific, the identification must be considered questionable. That being the case, the utility of the taxon as an index fossil must be questioned also.

LITHOLOGY AND DEPOSITIONAL ENVIRONMENT

Thin section analysis.—The rock in which the shrimp are preserved is a fissile, thinly laminated, brittle, silty shale, light grey on fresh surfaces and cream to light

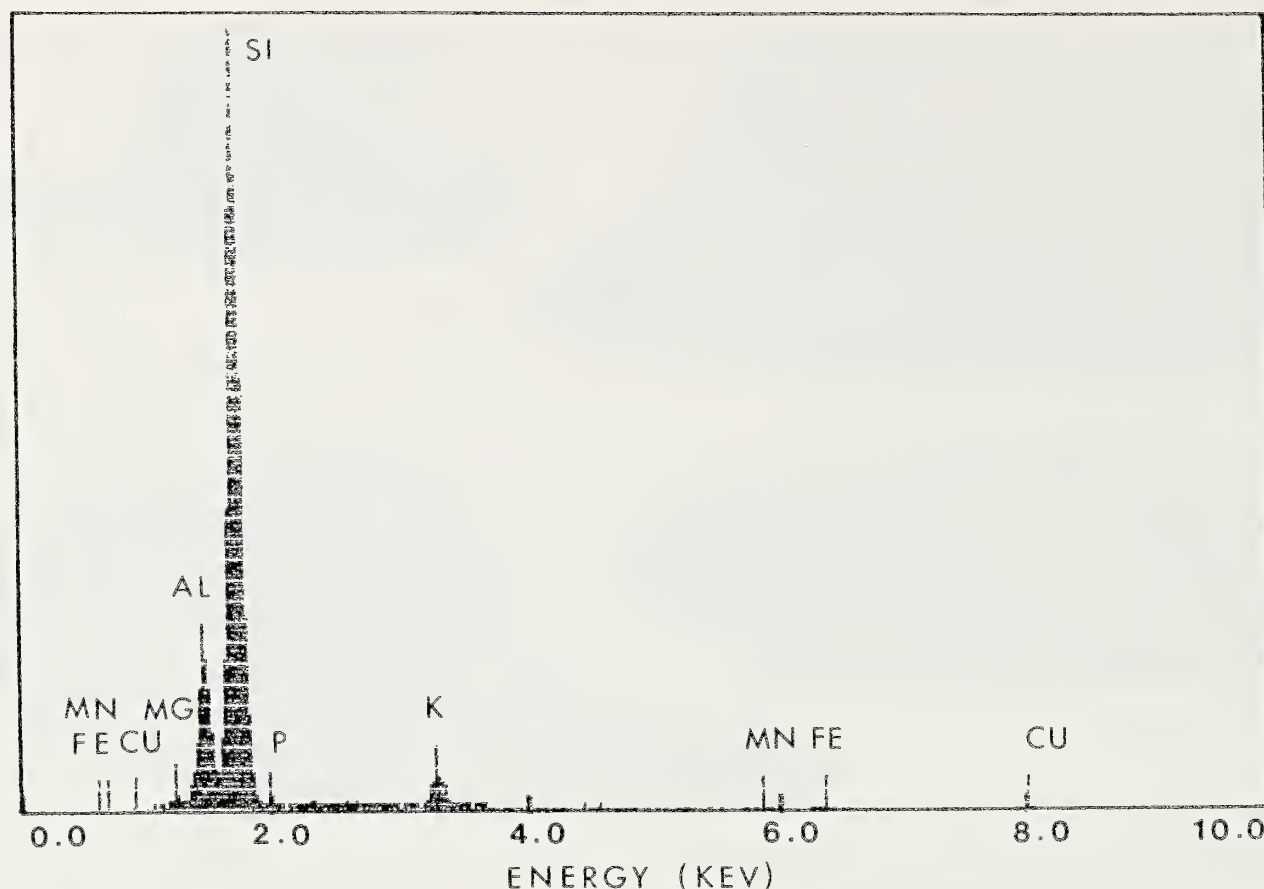


Fig. 7.—Energy dispersive X-ray pattern of sediment on bedding plane upon which *?Penaeus maddeni* was preserved.

tan on weathered surfaces. Sedimentary structures, such as ripple marks or bioturbation, are generally lacking. In thin section, the silt-sized grains appear to be well-sorted quartz grains. Other constituents include clay minerals and minor feldspar grains. The rock is poorly cemented, moderately indurated, and lacks calcium carbonate either as grains or cement. The individual laminae, distinguished on the basis of faint variations in color, are laterally continuous, parallel to planes of fissility and typically uniform in thickness (10–20 laminae per cm), except where draped over fossils or larger grains. Fossils in the rock samples include fish scales, vertebral centra, and isolated bones (probably fish), in addition to the shrimp. Microfossils are apparently lacking in the specimen. The fossil shrimp are densely concentrated on one or two discrete bedding planes within the rock samples.

Whole rock SEM analysis.—Chemical analysis of the specimens from the Loyola Formation was conducted by means of an ISI SX40 scanning electron microscope and Princeton Gammatech energy dispersive X-ray attachment. Analysis was conducted using a high voltage source of 30 kV. Several analyses were conducted in order to obtain high point counts and consistent results. This analysis revealed the specimens to be composed largely of silica and aluminum, with minor constituents of potassium and copper (Fig. 7). The silicon, aluminum, and potassium concentrations are consistent with the presence of the mineral muscovite. Copper concentrations are consistently low; this element is thought to be a minor constituent which is bound up in the small clay fraction of the specimen. The rock exhibits an alternating sequence of organic and silicic mud layers. No significant compositional deviation was found between the fossiliferous layers and non-fossiliferous layers of the rock.

SEM analysis of chitin.—Original chitinous material was difficult to discern in

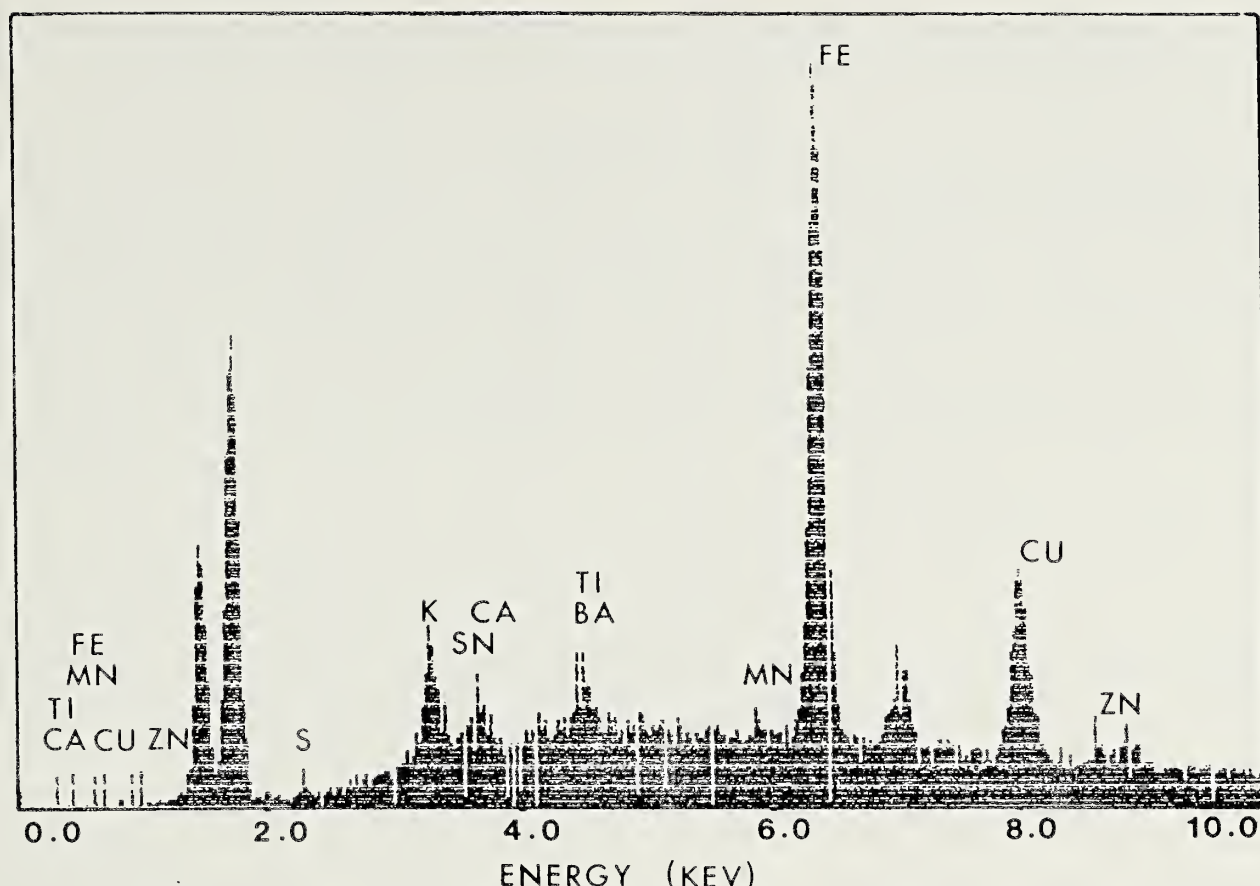


Fig. 8.—Energy dispersive X-ray pattern of cuticle sample from ?*Penaeus maddenii*.

the specimens under ordinary microscopic analysis. Nonetheless, material thought to be chitin from two different rock specimens was prepared for SEM/EDS analysis. Specimen #1 was less compressed than specimen #2, and had several thick (0.5 mm) sections of presumed chitin. Specimen #2 had been severely compressed and revealed abundant small filmy chitin remnants, some of which were very well preserved. Both specimens were analyzed repeatedly at 30 kV in order to obtain high point counts and consistent results.

EDS analysis of these samples revealed a concentration of trace metals and a background count higher than the rock samples. The most abundant constituents were iron and copper with minor amounts of zinc, nickel, and titanium (Fig. 8). Minute amounts of sulphur and calcium were also detected. Trace amounts of potassium were detected, but could not be separated from whole-rock composition.

ENVIRONMENTAL INTERPRETATION

General.—Analysis of the grain size, sorting, the uniformity in the range of sediment coloration, the lack of sedimentary structures, and the low degree of disarticulation of fossils in the rock samples support an interpretation of low energy conditions during deposition. The fine-grained nature of the bulk of the samples is indicative of a region of low depositional energy. The observed uniformity of coloration and the high degree of sediment sorting (uniformly fine grained) of individual layers is also indicative of very low energy conditions. The high degree of articulation of the fossilized shrimp remains would seem to indicate preservation under low energy conditions. If high energy conditions had prevailed, the remains would show a much higher degree of disarticulation due to reworking by wave or current action.

Depth.—The progression from sandstones and conglomerates directly into shales,

with no apparent break in deposition, is interpreted to be the result of marine incursion through the Gulf of Guayaquil, "the Ecuadorian portal," due to basin subsidence and sea level rise. Basin depth is controlled by subsidence. As the Loyola Formation approaches 360 m in thickness, subsidence could have equalled, or exceeded, that value. However, it is probable that much of the formation was deposited in a lacustrine setting, rather than a marine environment as is postulated for the lower part of the formation. If that is the case, subsidence and, therefore, maximum depth of deposition would have been less than 360 m. The sediments lack sufficient depth-indicating material, such as calcium carbonate, strontium, magnesium, and iron, to permit making a quantitative estimate of depth. In a qualitative sense, deposition of the shrimp-bearing beds occurred at a depth below wave base and above 360 m.

The alternating sequence of organic and silicic mud layers suggests shallow water deposition near an active source of siliciclastic sediment. The presence of silt grains in the silicic laminae precludes deposition beyond the reach of fluvial sediment, and the nature of the laminae suggests a low energy environment. Schram (1986) noted that most *Penaeus* were benthic inhabitants of shallow water which is consistent with a depth between wave base and 360 m.

Temperature.—Estimation of paleotemperature can be made using comparisons of temperature limitations of extant taxa related to those in the Loyola Formation, determining isotopic ratios of oxygen or carbon isotopes in suitable materials, or considering the paleogeographic setting in which the rocks were deposited. In this specific instance, only the latter approach is useful. The taxa found in the Loyola Formation and whose temperature range is known, *Diplodon* sp. and *Dorissa* sp., have rather non-restrictive temperature ranges (Camacho, 1966). The sediments lack calcium carbonate suitable for isotopic analysis. Thus, it is not possible to use analytical techniques on this material to determine paleotemperature. However, an estimate of high water temperature can be made based upon the equatorial position of Ecuador during the Miocene. A minimum temperature range of 25–28°C and be postulated for the surface water (Schopf, 1980). This range represents a minimum value because those are the temperatures of the open sea surface. A partially enclosed basin, such as the Cuenca Basin, most likely was even warmer.

Salinity.—The intermontane basins of the Sierra are characterized throughout the literature as "fresh water basins" (Bristow and Parodiz, 1982; Baldock, 1985). However, this is not consistent with the occurrence of ?*Necroneustes proavitus*, a marine crab (Bristow and Parodiz, 1982), and echinoid fragments (Erazo Vallejo, 1965) in the basal Loyola Formation. Penaeid shrimp also are confined to marine conditions (Glaessner, 1969). Thus, while the majority of the taxa of the Loyola Formation may be fresh water organisms (Bristow and Parodiz, 1982), the marine component strongly argues for deposition of some of the formation under marine conditions. Additional stratigraphic control is necessary to determine the precise relationship between the marine and nonmarine components.

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suggested that the specimens, if penaeids, might represent juveniles. Our sincere thanks to these people. Contribution 546, Department of Geology, Kent State University, Kent, Ohio 44242.

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REDESCRIPTION OF *SPHODROSAURUS PENNSYLVANICUS*
COLBERT, 1960 (REPTILIA) AND A REASSESSMENT
OF ITS AFFINITIESHANS-DIETER SUES¹

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ABSTRACT

Sphodrosaurus pennsylvanicus Colbert, 1960 from the Upper Triassic of Lancaster County, Pennsylvania, was originally classified as a procolophonid. The holotype and only known specimen is preserved in a hornfelsed mudstone of the Hammer Creek Formation, which may be early Norian in age. The recently prepared holotype is a natural mold of a partial skull and skeleton and was restudied using high-fidelity latex rubber casts. The alleged cranial frill comprises the posterior ends of both mandibular rami. The atlanto-occipital joint is placed well forward of the jaw articulation. The centra of the cervical and most of the dorsal vertebrae have strongly developed mid-ventral keels. *Sphodrosaurus* is clearly not a procolophonid, but it can be referred to the Diapsida on the basis of several skeletal features. Its affinities within Diapsida, however, remain unresolved, although it is probably a neo-diapsid.

INTRODUCTION

Colbert (1960) described the partial skull and postcranial skeleton of a small reptile, preserved for the most part as a natural mold in a block of hornfelsed mudstone of Late Triassic age from a quarry east of Bowmansville in Lancaster County, Pennsylvania (see below). Following preliminary identification of the fossil as a specimen of *Hypsognathus fenneri* Gilmore, 1928 by the late David Dunkle (then at the United States National Museum), Colbert assigned it to the Procolophonidae, but he designated it as the holotype of a new genus and species, *Sphodrosaurus pennsylvanicus*. His assessment was subsequently accepted by Kuhn (1969) and Ivakhnenko (1979) in their systematic reviews of the Procolophonia. Baird (1986) first pointed out that *Sphodrosaurus* was not a procolophonid, and he suggested rhynchosaurine affinities instead. At his suggestion, Olsen borrowed the holotype from the North Museum of Franklin and Marshall College. He carefully removed the poorly preserved bone adhering in some parts of the natural mold in preparation for casting it using high-fidelity flexible compounds. Recently prepared latex rubber casts reveal many new details of the structure of the specimen (which previously had not been prepared) and form the basis for our redescription of *Sphodrosaurus pennsylvanicus* and reassessment of its affinities.

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Colbert (1960) explicitly compared *Sphodrosaurus pennsylvanicus* to the only North American procolophonid then described, *Hypsognathus fenneri* Gilmore, 1928. *Hypsognathus* was originally known only from the Upper Triassic (Norian) Passaic Formation (formerly Lower Brunswick Formation) of the Newark basin of the Newark Supergroup in New Jersey (Gilmore, 1928; Colbert, 1946). Subsequently, this taxon was also recorded from the New Haven Arkose of Connecticut and the upper Wolfville Formation of Nova Scotia (Olsen, 1980; Baird, 1986). Although confident in assigning *Sphodrosaurus* to the Procolophonidae, Colbert noted that it differed from other known taxa of that group in a number of features, especially the hindlimb.

GEOLOGICAL SETTING

The block bearing the holotype of *Sphodrosaurus pennsylvanicus* came from what was already in the mid-1950s an inactive quarry described as “. . . on the Honeybrook quadrangle, one-fourth inch above the ‘B’ in ‘Brecknock,’ Brecknock Township, Lancaster County” (Price, 1956:168). The quadrangle in this reference is that published by Bascom and Stose (1938), rather than a standard 7.5 minute United States Geological Survey quadrangle. Olsen has relocated the old quarry adjacent to the north side of Yellow Hill Road, about 200 m E of its intersection with Oaklyn Road. Latitude and longitude are approximately 40°11'45"N and 75°59'50"W. This position is about 1.4 km E of Bowmansville, Lancaster County, Pennsylvania.

In the vicinity of Bowmansville, massive intrusions of diabase plutons of Early Jurassic age have extensively altered surrounding sedimentary rocks. The old quarry is located in gray hornfelsed mudstone near one of these intrusive bodies within the Hammer Creek Formation sensu Glaeser (1963). The Hammer Creek Formation itself consists of thick sequences of brown and red conglomerate and pebbly sandstone that alternate with thinner sequences of red mudstone. The formation links the contemporaneous Passaic Formation of the Newark basin to the east with the Gettysburg Shale of the Gettysburg basin to the west. Based on an average dip of 20°, the locality is stratigraphically situated about 1.4 km above the top of the Stockton Formation and about 1.6 km above the pre-Newark contact. The exact stratigraphic position relative to the well-known sequence in the Newark basin, however, is uncertain (Fig. 1).

The mapped distribution of the mudstone sequence from which the fossil originates can be traced along strike to the northeast where it meets the Birdsboro diabase dike. Based on the mapped offset of the position of the Lockatong Formation pinch-out on the east and the boundary between the Stockton and Hammer Creek formations on the west side of the dike, the stratigraphic position of *Sphodrosaurus pennsylvanicus* should be between the upper Lockatong Formation and the Graters Member of the Passaic Formation, most likely somewhere close to member D or E–F (Fig. 1). This would place it close to the Carnian–Norian boundary, possibly early Norian (Cornet, 1977; Fig. 1).

The mudstones of the Hammer Creek Formation have not been well studied. The generally laterally persistent, thin beds (at the quarry scale) indicate a primarily lacustrine depositional environment for many of the finer-grained units. This is consistent with inferences concerning a lacustrine origin for most of the fine-grained intervals of both the contemporaneous and contiguous Passaic and Gettysburg formations (Olsen, 1986; Smoot, 1991).

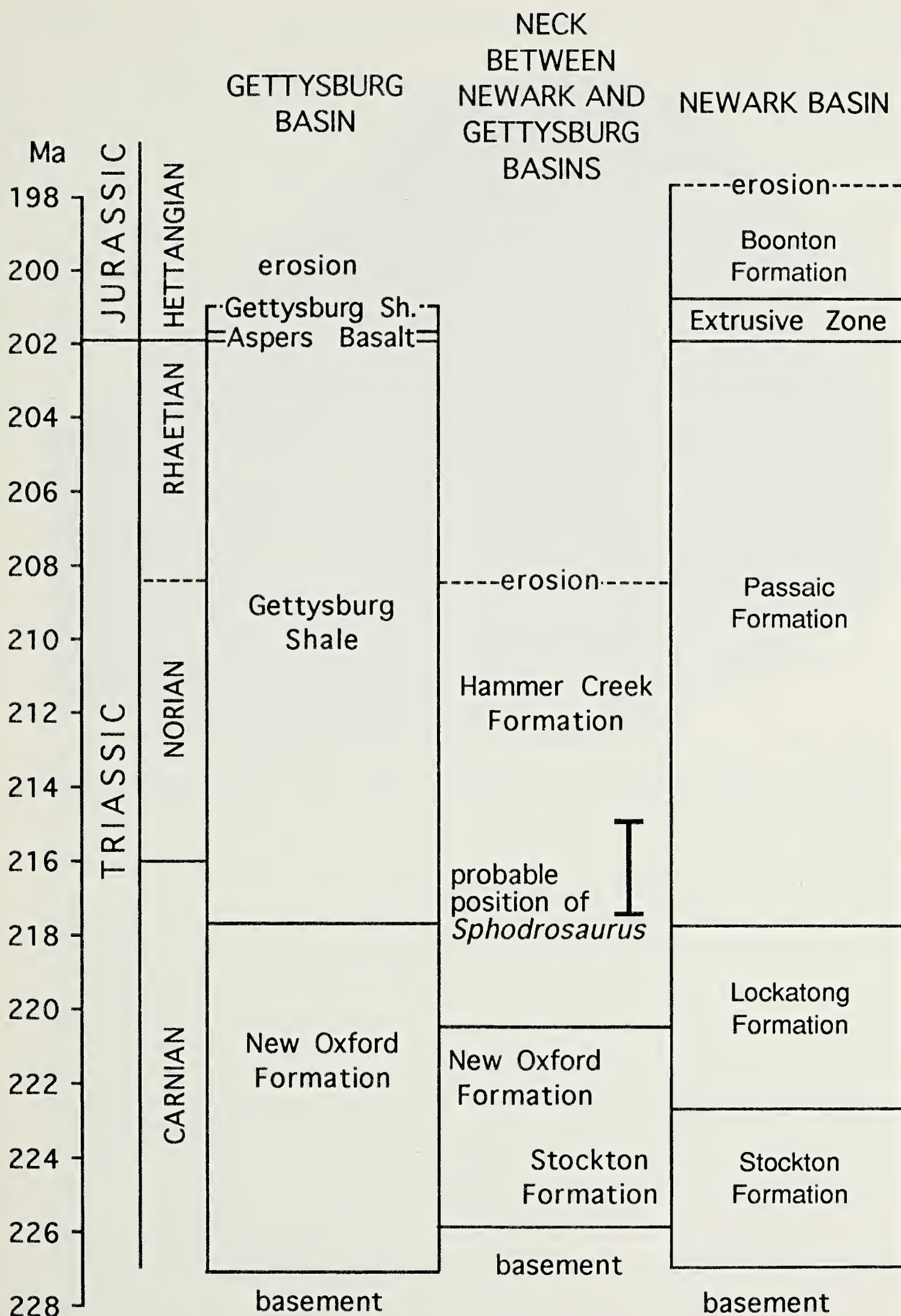


Fig. 1.—Probable stratigraphic position of the *Sphodrosaurus* horizon. Time scale and stratigraphic correlations are modified from Olsen et al. (1989).

SYSTEMATIC PALEONTOLOGY

Class Reptilia

Subclass Diapsida

Order Neodiapsida *incertae sedis*Genus *Sphodrosaurus* Colbert, 1960

Type species.—*Sphodrosaurus pennsylvanicus* Colbert, 1960 (by monotypy).

Revised diagnosis.—Head proportionately very large. Atlanto-occipital joint apparently situated well anterior to jaw joint. External surface of posterior mandibular bones distinctively sculptured with longitudinal ridges and grooves. Centra of cervical and more anterior dorsal vertebrae with strongly developed mid-ventral keels. This combination of characters has not been found in any other known diapsid.

Sphodrosaurus pennsylvanicus Colbert, 1960

Sphodrosaurus pennsylvanicus Colbert, 1960: 2.

Holotype and only known specimen.—Franklin and Marshall College, North Museum, no. 2321, natural mold of a partial skull and postcranial skeleton exposed in ventral view (Fig. 2, 3). Found by Norman Waltz before 1956 and brought to the North Museum on 24 February 1956.

Type locality and horizon.—See above.

Age.—Late Triassic (?early Norian).

Diagnosis.—Type and only known species of genus as diagnosed above.

DESCRIPTION

The specimen is preserved as a natural mold of a largely articulated partial skeleton in ventral view. Due to natural discoloration, the impression of the skeleton is lightly colored and thus readily visible against the surrounding dark gray hornfelsed mudstone (Fig. 2). The fossil comprises the posterior region of the skull and mandible, the postcranial axial skeleton back to the sacral region, gastralia, parts of the pectoral girdle and both forelimbs, the left pubis and right pelvic bones, and most of the right hindlimb (Fig. 3).

Skull and mandible.—Colbert (1960) correctly noted the unusually large size of the skull relative to the body. Only the rather wide posterior region of the skull is preserved. A “long expanse of sculptured bone on each side” was interpreted by Colbert (1960:8) as representing “the lower damaged edges of the quadratojugals, squamosals, and tabulars.” He regarded them as part of a frill along the back of the skull over the cervical region. Preparation revealed that these structures actually represent the posterior ends of the two mandibular rami (Fig. 3, mr). The ventral margin of each ramus forms a sharp, somewhat inturned edge. The external surface is irregularly sculptured with longitudinal ridges and grooves. The truncated posterior end of each jaw ramus comprises articular and prearticular; the suture between these bones is only visible in posterior view. There is no distinct retroarticular process. In the basicranial region, Colbert (1960:9) noted the presence of bone, which he interpreted as “in part the opisthotic, with perhaps other elements (perhaps the proötic) joining it” and which he labelled as the right proötic in his illustration (Colbert, 1960:fig. 6). We identify this bone as the right pterygoid (Fig. 3, pt). The transverse process of this element is visible along the top edge of the block, and its quadrate flange can be traced posterolaterally, where it probably contacts the quadrate. A portion of the left pterygoid is also exposed.

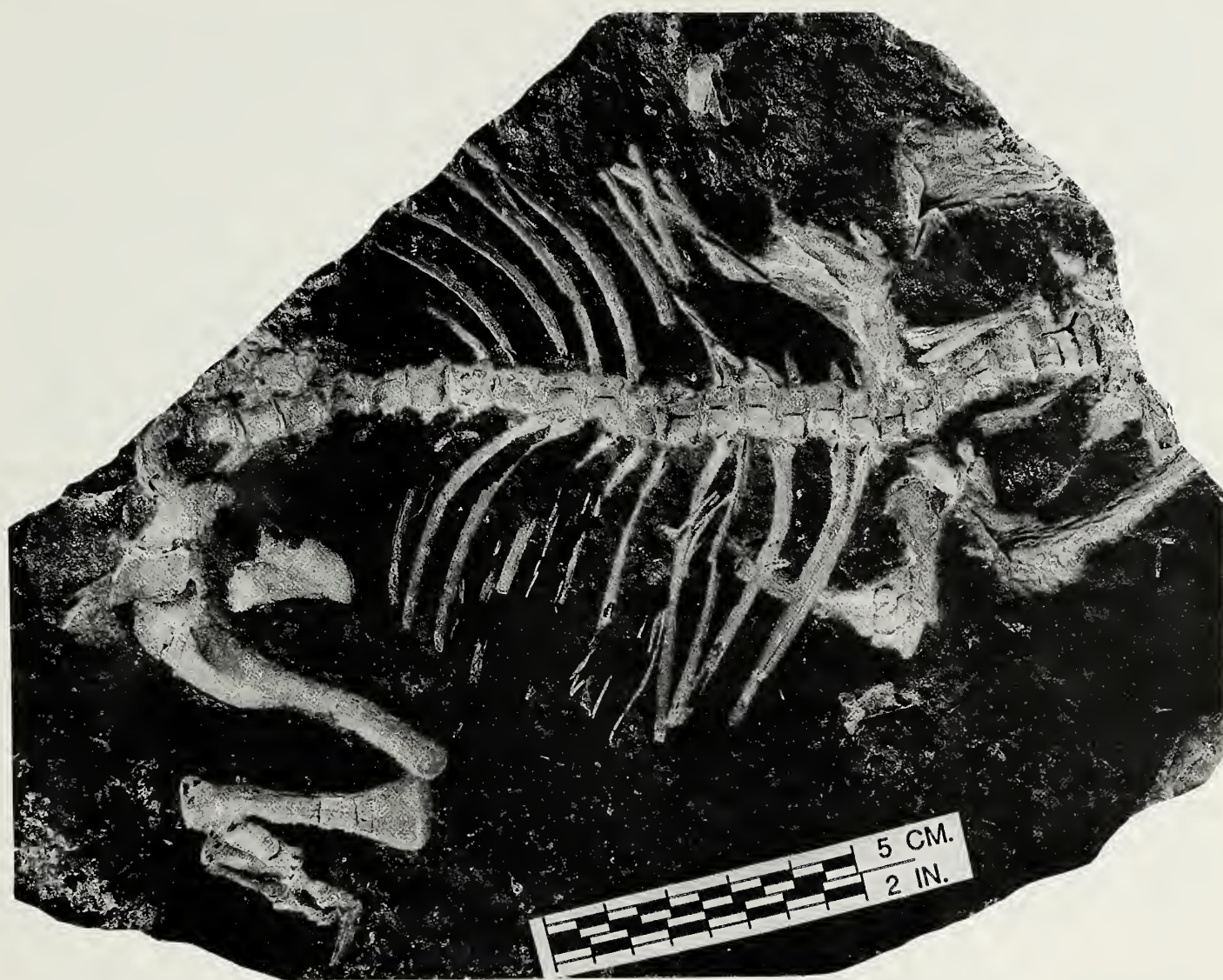


Fig. 2.—Natural mold of the partial skeleton of *Sphodrosaurus pennsylvanicus* Colbert, 1960 (North Museum, Franklin and Marshall College, no. 2321, holotype) after completed preparation.

Most of the basicranial region is not preserved. The atlanto-occipital joint, however, appears to be placed well forward of the jaw articulation. Although some postmortem displacement of the mandible posteriorly cannot be entirely ruled out, it seems that the quadrate flange of the pterygoid and the pterygoid flange of the quadrate have not been displaced.

Vertebrae and ribs.—Colbert (1960:9) reported 26 vertebrae in a more or less articulated series between the skull and pelvis, of which 25 are said to be presacrals. After preparation, we count only a total of 22 post-atlantal centra, all of which are exposed in ventral view (contra Colbert). Details of the atlanto-occipital region are unclear. Colbert noted a “large broad spine” on the axis, which he interpreted as the neural spine of that vertebra but which actually represents a separate piece of bone of uncertain identity. Intercentra are absent. Starting at the axis, the anterior 16 vertebral centra possess strongly developed longitudinal, mid-ventral keels, which begin to diminish at the 19th vertebra. The amphicoelous centra bear prominent, raised parapophyseal facets anteriorly. Their anterior and posterior articular ends have distinct rims. The centra of the post-axial cervical vertebrae are shorter than those of the dorsals. The centrum of the last preserved vertebra probably represents a sacral, as suggested by Colbert, and there is an apparent sacral rib adjacent to it on the right side.

Several long cervical ribs (Fig. 3, cr) extend parallel to the second to fifth vertebra

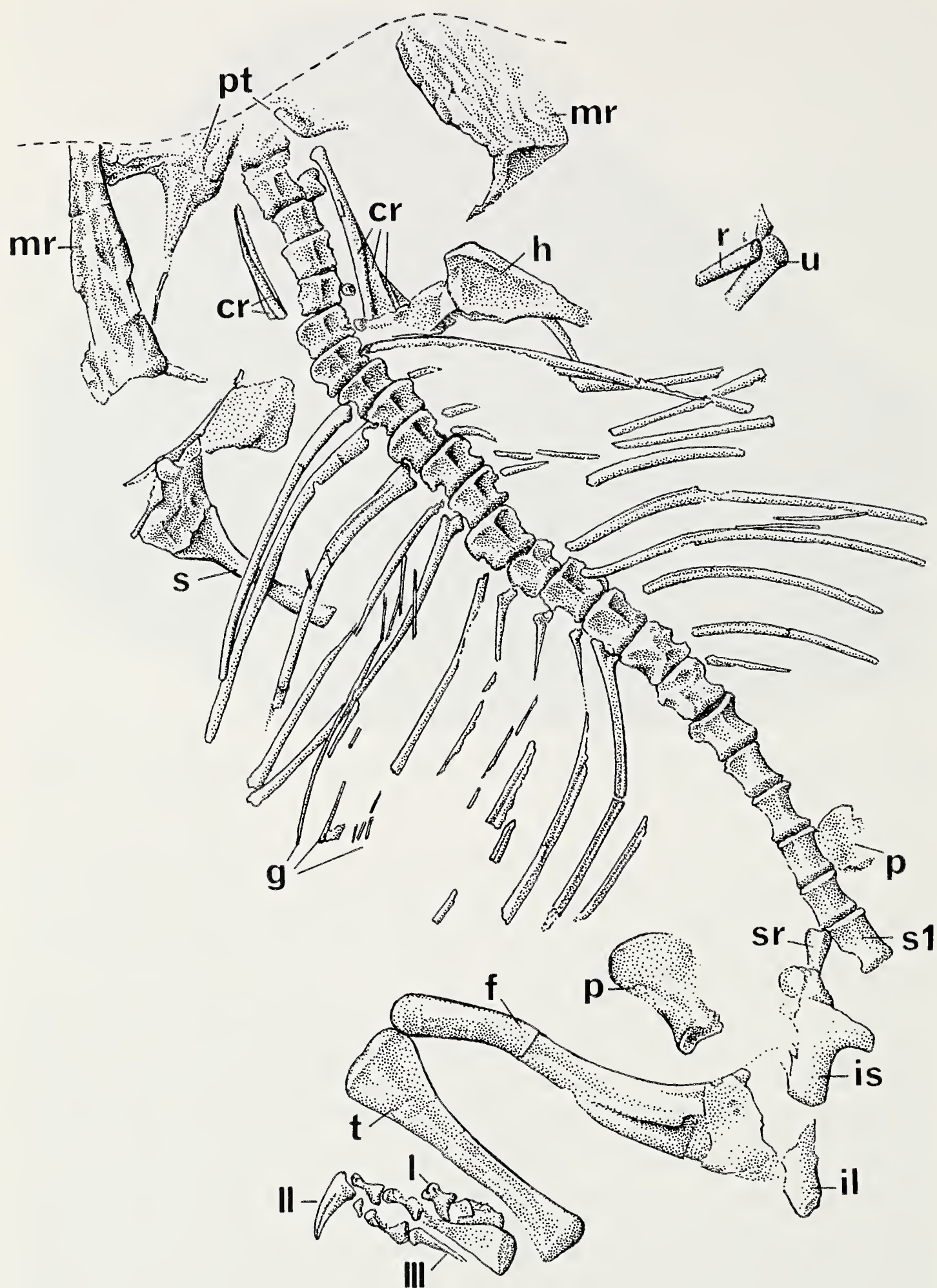


Fig. 3.—*Sphodrosaurus pennsylvanicus* Colbert, 1960, drawing based on a latex peel of the holotype. Abbreviations: cr, cervical ribs; f, femur; g, gastralia; h, humerus; il, ilium; is, ischium; mr, mandibular ramus; p, pubis; pt, pterygoid; r, radius; s, scapula; s1, sacral vertebra 1; sr, sacral rib; t, tibia; u, ulna; I-III, pedal digits I-III. Scale bar equals 2 cm.

on each side; their anterior ends are not visible. The long, slender dorsal ribs are only slightly curved, indicating a broad trunk region. The rib-heads are not clearly exposed, and it is impossible to ascertain from the casts whether they are dichcephalous or holocephalous. Fragments of very slender, rod-like gastralia (Fig. 3, g) are preserved in several places of the mid-trunk region. There is no evidence of dermal armor.

Pectoral girdle and forelimb.—The scapula (Fig. 3, s) has a tall, slightly recurved, and apparently slender blade, which is exposed between several ribs on the right side. Details of the base of the scapula and the coracoid region are obscured by crushing. The humerus, partially exposed on both sides but most clearly visible on the left side (Fig. 3, h), has a broad proximal end merging into a narrow shaft; its distal portion is buried in the matrix on either side. Radius (r) and ulna (u) are only documented by the associated distal portions of the left elements (Fig. 3). The distal end of the ulna has a convex surface for articulation with the carpus.

Pelvic girdle and hindlimb.—The right ilium, right ischium, and both pubes are preserved (Fig. 3). The ilium (il) preserves few unambiguous details. The ischium (is) and pubis (p) are both large, plate-like bones. The right hindlimb is sharply flexed at the hip, knee, and ankle. Colbert correctly noted that it is long, in its extended position subequal in length to the entire presacral vertebral column. The femur (Fig. 3, f), exposed in posterior view, is approximately 57 mm long and equal in length to about nine posterior dorsal centra. Its fairly slender shaft is sigmoidally curved. The damaged proximal head of the femur is large and inturned dorsomedially. The medial distal condyle projects ventrally. A prominent ventral ridge is developed on the proximal half of the femur. The slightly crushed tibia (Fig. 3, ti), exposed in medial view, is robust and distinctly shorter than the femur (39 mm vs. c. 57 mm).

No unambiguous tarsal elements are preserved. Parts of three digits of the right pes are exposed in ventromedial view (Fig. 3, I–III). The first metatarsal, which overlaps the second proximally, is flattened, roughly quadrangular, and 8.5 mm long. Its broad distal ginglymus is set at an angle of about 50° to the shaft, indicating that the hallux diverged medially. A stout phalanx articulates with metatarsal I; ventral to it there is a trace of an ungual that is buried deeper in the rock. Metatarsal II is concealed medially and distally, the exposed portion being 15 mm long; it is broad proximally and rapidly narrows to a slender waist more distally. The second pedal digit has three phalanges including a sharply pointed ungual that is long and straight and bears a distinct lateral groove for the horny sheath of the claw. The lateral edge of metatarsal III is exposed for a length of about 13 mm but its proximal end is concealed. Articulating in sequence with it are a long first phalanx and the proximal end of the second. The fourth and fifth digits are not exposed. The pes was probably more or less equal in length (in its fully extended position) to the tibia.

AFFINITIES OF *SPHODROSAURUS PENNSYLVANICUS*

The mode of preservation of the holotype and only known specimen of *Sphodrosaurus pennsylvanicus* leaves very few anatomical features for assessing its phylogenetic position. We found no derived characters to support reference of this taxon to the Procolophonidae. Colbert (1960:17–18) cited “size, the obviously large skull, the extension of the back of the skull in a sort of frill over the cervical region, the evidently broad vertebral neural arches (as indicated by the separation of the heads of the ribs), and the holocephalous, flaring ribs” in support of procolophonid affinities. Aside from the phylogenetically uninformative size crite-

rion, we have demonstrated above that the alleged frill is based on what are actually the posterior ends of the mandibular rami. The inferred width of the neural arches is of questionable diagnostic value. The nature of the proximal articular end of the trunk ribs is unclear, but holocephalous ribs are also present in most diapsid reptiles (Laurin, 1991).

As Colbert recognized, several features clearly distinguish *Sphodrosaurus* from known procolophonid taxa. These characters indicate diapsid affinities. The rather slender femur with its sigmoidally curved shaft is the only observable character to support reference of *Sphodrosaurus* to the Neodiapsida as diagnosed by Benton (1985). Although the distal portion of the left humerus is not completely exposed, it is apparent from the proportions of the left forelimb that it was distinctly shorter than the femur, much as in neodiapsids (Laurin, 1991). The strongly developed mid-ventral keeling on the cervical and more anterior dorsal centra of *Sphodrosaurus* also indicates diapsid affinities (although at least the centra of the more anterior dorsal vertebrae in *Hypsognathus fenneri* also bear mid-ventral keels; Sues, personal observation), but most diapsid reptiles except *Araeoscelis* (Laurin, 1991) show less pronounced keeling. The phylogenetic significance of the absence of a retroarticular process is uncertain (see Laurin, 1991).

Baird's (1986) reference of *Sphodrosaurus* to the Rhynchosaurinae was based on the position of the atlanto-occipital joint well forward of the jaw joint. This condition is unlike that found in the Procolophonidae (Ivakhnenko, 1979). It is present not only in rhynchosaurine rhynchosaurs (Benton, 1990), but also in various other Triassic archosauromorph reptiles such as *Erythrosuchus* (Huene, 1911) and *Proterosuchus* (Broili and Schröder, 1934; Cruickshank, 1972). The holotype of *S. pennsylvanicus* preserves none of the other features considered diagnostic for Rhynchosauria by Benton (1990), and we found no derived characters in support of reference to the Archosauromorpha (as diagnosed by Benton, 1985) in general.

Possibly diagnostic features of *Sphodrosaurus pennsylvanicus* include the proportionately very large head, the well-developed, distinctive sculpturing composed of longitudinal ridges and grooves on the external aspect of (at least) the posterior mandibular bones, the strongly developed mid-ventral keeling of the cervical and more anterior dorsal centra, and the great width of the trunk region. *Sphodrosaurus* does not closely resemble any other known early Mesozoic diapsid and represents one of a growing number of tetrapods from the Triassic portion of the Newark Supergroup of eastern North America that defy placement in currently recognized higher taxa. Additional material is clearly needed to clarify the affinities of this distinctive little reptile.

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REVIEW OF THE GENUS *ADRIMUS* BATES, 1872
(INSECTA: COLEOPTERA: CARABIDAE: PTEROSTICHINI)STEFANO L. STRANEO¹

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ABSTRACT

The taxonomic position of the Neotropical genus *Adrimus* Bates among pterostichines is discussed. A key to species is presented. Eleven new species are described: *Adrimus claripes* (Brazil), *A. latibasis* (Argentina), *A. suturalis* (Brazil), *A. elytralis* (Bolivia), *A. ventralis* (Brazil), *A. balli* (Brazil), *A. proximus* (Paraguay), *A. longior* (Brazil), *A. paulensis* (Brazil), *A. matoanus* (Brazil), and *A. irideus* (Argentina).

INTRODUCTION

The Neotropical carabid genus *Adrimus* was described by Bates (1872:176) to include pterostichines very closely related to the species of *Loxandrus* LeConte. As in *Loxandrus*, species of the genus *Adrimus* lack a scutellar stria on each elytron and have a single puncture at about mid-length on the third elytral interval. All species of *Adrimus* have a complete anterior submarginal border which is greatly widened in the middle and separated from the pronotal disc by a very deep sulcus, but this character state is also found in a few species of *Loxandrus*. Thus the only differences between the two genera are: the three basal protarsomeres of male *Loxandrus* (Fig. 1) are obliquely dilated to the inside (medial or anterior to the protarsal midline), whereas in *Adrimus* (Fig. 2) the three basal male protarsomeres are equally dilated on both sides of the protarsal midline as in most pterostichines; the metepimera of *Adrimus* species are very short and truncated at the apex (Fig. 3), whereas in *Loxandrus* (Fig. 4) they are longer and rounded at the apex. Keys to the genera of Neotropical Pterostichini are in Straneo (1977, 1979), and Neotropical *Loxandrus* were revised by Straneo (1991).

From what little is known about the ecology of *Adrimus* species, it appears to be similar to that of *Loxandrus*. Individuals are found near watercourses and wet places, often under the bark of logs or dead trees. They are often drawn to white or ultraviolet light, but always near damp locations. The genus *Loxandrus* is widespread, with many species in Australia, Sulawesi, South and Central America, the West Indies, and the southern portion of North America. The species differ greatly in size, shape and color, and many species have been collected in great numbers. The genus *Adrimus*, on the other hand, is confined to a few regions in South America (except for one species from Guatemala), and specimens are relatively rare. The species are all very similar in size, shape and color. One species reaches 11 mm in length, but the others are between 6 and 9 mm in length. Females predominate among specimens collected at light.

The identification of species of *Adrimus* is difficult. I have found only the following characters to be useful: size, color of legs or (in a few species) of dorsal surface or abdominal apex, dimensions of eyes, shape of pronotum and elytra, and relative size of pronotum compared with elytra. I do not use the shape of the

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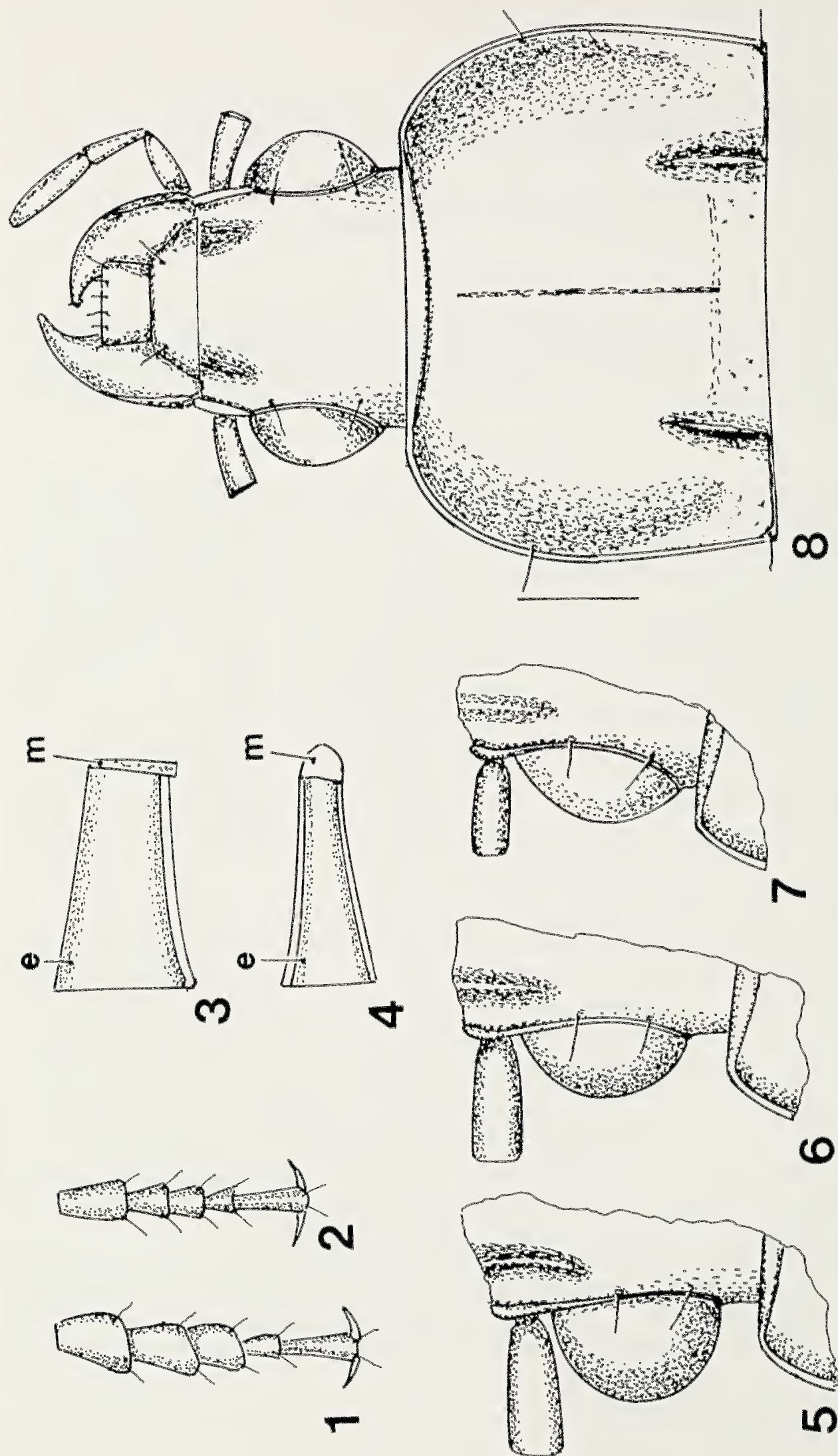


Fig. 1-8.—Diagnostic features of *Adrimus* and *Loxandrus* species. 1, protarsus of male *Loxandrus*; 2, protarsus of male *Adrimus*; 3, metepisternum (e) and metepimeron (m) of *Adrimus*; 4, metepisternum (e) and metepimeron (m) of *Loxandrus*; 5, eyes of *Adrimus* showing very convex, almost hemispherical outline; 6, eyes of *Adrimus* showing moderately convex outline; 7, eyes of *A. proximus* showing relatively flat outline; 8, head and pronotum of *A. uruguaicus* (scale line = 1 mm).

aedeagus in the key and the descriptions of species. For many species of *Adrimus*, males are not known. In known males, I have found that the aedeagus is very poorly sclerotized and very uniform in shape, without appreciable differences between species.

The following species have already been described:

- Adrimus fuscipes* (Brullé, 1834) (described as *Drimostoma fuscipes*, recognized by Chaudoir (1872:13) as belonging to *Adrimus*)
- A. viridescens* (Bates, 1871) (described in *Loxandrus*)
- A. creperus* Bates, 1872
- A. geminatus* Bates, 1872
- A. microderus* Bates, 1872
- A. rufangulus* Bates, 1872
- A. olivaceus* Bates, 1882
- A. aenescens* Tschitschérine, 1900
- A. affinis* Tschitschérine, 1900
- A. virens* Tschitschérine, 1901
- A. uruguaicus* Tschitschérine, 1903

Reports of *Adrimus* in the entomological literature are scarce. Reichardt (1977:408) cited *Adrimus* as a genus near *Loxandrus* that included ten species. In my keys to South American genera of Pterostichini (Straneo, 1977, 1979), *Adrimus* was placed near *Loxandrus* and separated from it by the shape of the metepimera. In those papers, I erroneously included *Adrimus* among the Pterostichini with male basal protarsomeres obliquely dilated, an error which I correct here. Tschitschérine (1900:244) partially redescribed *A. fuscipes* (Brullé) and wrote that many other species remained to be discovered. Bates (1882) also noted that specimens of *Adrimus* are rare. Indeed, among many thousands of South American pterostichines I have received for identification over a 40-year period, I have seen until recently only a very few specimens of *Adrimus*. In the last few years I have seen about 50 additional specimens among undetermined material presented to me by my late friend Jacques Nègre, and among undetermined specimens lent to me by several institutions.

The study of this new material with the specimens already in my collection and aided by examination of the types of two poorly known species, *A. fuscipes* (Brullé) and *A. uruguaicus* Tschitschérine, revealed numerous undescribed species. This induced me to publish this review, which I consider highly provisional as further collecting in South America will no doubt produce additional new species.

To facilitate identification, the species of *Adrimus* have been informally divided into two groups. Group One includes black or blackish-brown species without metallic tinges or coloration. Group Two includes species with the upper surface (at least of the elytra) with distinct metallic coloration, generally green, greenish or aeneous. The species of Group Two are less familiar to me. To make the key as complete as possible, I have interpreted the names of species in Group Two according to the original descriptions, supplemented, in some cases, by identified material in my collection. All of the new species described herein belong in Group One, and I have seen the types of two of the three previously described species. Thus in Group One only *A. rufangulus* Bates is interpreted from the original description.

Material studied is in the following collections: Carnegie Museum of Natural History (CMNH); Collection Straneo (CS); Fundación Miguel Lillo, Tucumán (FMLT); and University of Alberta, Strickland Museum (UASM). The type of *A.*

fuscipes (Brullé) was borrowed from the Muséum National d'Histoire Naturelle de Paris, and the type of *A. uruguaicus* Tschitschérine was borrowed from the Institut Royal des Sciences Naturelles de Belgique. I indicate by r_d (*ratio dimensionum*) the ratio between length and width of an insect or any of its parts; aw = anterior width; bw = basal width; gw = greatest width.

Key to Adults of *Adrimus*

1. Entire upper surface black or dark brown without metallic coloration (Group One) 2
- 1'. Upper surface (at least elytra) with evident metallic coloration, green, greenish or brassy (Group Two) 16
- 2(1). Eyes very convex (Fig. 5); legs entirely ferrugineous 3
- 2'. Eyes moderately convex or not very convex (Fig. 6, 7); legs brown or ferrugineous 4
- 3(2). Pronotum obviously narrowed toward base (Fig. 9); lateral border narrower; sides subsinuate before basal angles; size 8 mm; Brazil: Alagoas *Adrimus claripes*, new species
- 3'. Pronotum less narrowed toward base (Fig. 10); lateral border wider; sides not subsinuate before basal angles; size 8.5 mm; Argentina: Salta *Adrimus latibasis*, new species
- 4(2'). Elytra with posterior half of sutural interval and small portion of apical margin ferrugineous; under surface at least partly ferrugineous brown; size small (6–6.5 mm) 5
- 4'. Suture intervals concolorous with rest of elytra 6
- 5(4). All elytral striae equally impressed; pronotum shaped as in Fig. 11, sides subsinuate toward base; upper surface blackish-brown, shiny; legs ferrugineous; Brazil: Santarem *Adrimus suturalis*, new species
- 5'. First four elytral striae deep and entire, first four intervals moderately convex, remaining striae deep at base and apex, evanescent at middle; pronotum as in Fig. 12, sides not subsinuate toward base; upper surface black, shiny, subiridescent; legs lighter; Bolivia *Adrimus elytralis*, new species
- 6(4'). Larger (10.5–11 mm); upper surface piceous, shiny, slightly iridescent, base of antennae and legs (except tibial apex) testaceous red; pronotum transverse, sides slightly arcuate, slightly narrowed behind, base with coarse punctures, basal angles and lateral margins near base light red; abdomen piceous; elytral striae deep, punctate; Brazil: Ega *Adrimus rufangulus* Bates
- 6'. Smaller (9 mm or less) 7
- 7(6'). All elytral striae deeply and uniformly impressed; intervals moderately or strongly convex both on disc and laterally 8
- 7'. Only inner striae deeply impressed, inner intervals convex, outer striae deeply impressed at base and apex, shallower and finer toward middle, outer intervals flat 15
- 8(7). Pronotum subcordate, anterior angles strongly deflected 9
- 8'. Pronotum not subcordate, at most a little narrowed posteriorly, sides not sinuate toward basal angles; pronotum in most species more transverse 10
- 9(8). Dorsal surface piceous brown, elytra not or slightly iridescent; pronotum (Fig. 14) less narrowed posteriorly, basal angles slightly ob-

- tuse, some faint punctures at basal angles and middle of base; elytral striae moderately deep, intervals 2–3 moderately convex, 4–7 less convex at middle, all intervals convex at apex; length 7.8–8.5 mm; French Guiana *Adrimus fuscipes* (Brullé)
- 9'. Dorsal surface black, iridescent; pronotum longer, more narrowed posteriorly, basal angles square, impunctate, middle of base with many large punctures; elytral striae deep, intervals convex, especially lateral ones; length 9 mm; Brazil: Ega *Adrimus microderus* Bates
- 10(8'). Legs light ferrugineous; antennae dark brown with basal antennomeres ferrugineous; upper surface black, pronotum and elytra with narrow ferrugineous border, abdominal apex ferrugineous; elytra shiny, iridescent, deeply striate, disc slightly convex; pronotum as in Fig. 15; size 6.7–8 mm; Brazil: Alagoas *Adrimus ventralis*, new species
- 10'. Legs brown or at least with femora and trochanters darker than tibiae 11
- 11(10'). Less slender species (r_d of body = 2.35, r_d of elytra = 1.38); pronotum with sides strongly rounded (Fig. 16), pronotum greatly narrowed anteriorly and posteriorly (aw/gw = 0.68, bw/gw = 0.80); eyes large but moderately convex (Fig. 6); elytral striae deep, nearly impunctate; size 7.7 mm; Brazil: Pará *Adrimus balli*, new species
- 11'. More slender species (r_d of body = 2.43–2.58) 12
- 12(11'). Pronotum (Fig. 17) more narrowed anteriorly (aw/gw = 0.59), transverse (r_d = 0.68), space between basal impressions and hind angles nearly flat; elytra relatively short (r_d = 1.40); eyes flatter (Fig. 7); Paraguay: Dept. Central *Adrimus proximus*, new species
- 12'. Pronotum less narrowed anteriorly (aw/gw = 0.67–0.74) 13
- 13(12'). Pronotum (Fig. 18, 19) longer (r_d = 0.73–0.75), less narrowed anteriorly (aw/gw = 0.73–0.74) and more narrowed toward base (bw/gw = 0.87–0.89) 14
- 13'. Pronotum (Fig. 8) more transverse (r_d = 0.67), strongly narrowed anteriorly (aw/gw = 0.67), very little narrowed toward base (bw/gw = 0.93); Uruguay *Adrimus uruguaicus* Tschitschérine
- 14(13). Elytra more elongate (r_d = 1.55); pronotum as in Fig. 18; elytral epipleura and lateral border of pronotum black; size 8.7 mm; Brazil: Santa Catarina *Adrimus longior*, new species
- 14'. Elytra shorter (r_d = 1.45); pronotum as in Fig. 19; elytral epipleura and lateral border of pronotum reddish; size 8.8 mm; Brazil: Estado São Paulo *Adrimus paulensis*, new species
- 15(7'). Smaller (6.7 mm), less convex; head and pronotum blackish-brown, elytra black, not iridescent, antennae blackish with ferrugineous scape; pronotum as in Fig. 20; elytra elongate (r_d = 1.80) with disc flat; Brazil: Mato Grosso *Adrimus matoanus*, new species
- 15'. Larger (8.5 mm), more convex; upper surface black, shiny and iridescent on elytra, lateral border of pronotum brown, especially near basal angles; pronotum as in Fig. 21; elytra shorter, more convex (r_d = 1.47); Argentina: Entre Rios *Adrimus irideus*, new species
- 16(1'). Pronotum little narrowed toward base with sides not or slightly convergent behind 17
- 16'. Pronotum with sides more uniformly rounded or more strongly narrowed toward base 19

- 17(16). Upper surface bronze with suture and lateral margins of elytra reddish; pronotum very transverse, much narrower than elytra, with lateral border not flattened at basal angle, sides with very narrow light-colored margin; size 8 mm; Brazil: Pará . . . *Adrimus creperus* Bates
- 17'. Elytra unicolorous, without reddish suture and lateral margins; species from Guatemala and Venezuela 18
- 18(17'). Flatter, less convex; upper surface olivaceous bronze; basal angles of pronotum moderately raised, anterior angles very near to neck, base with coarse scattered punctures; elytra deeply striate, striae finely punctulate; size 9.5 mm; Guatemala . . . *Adrimus olivaceus* Bates
- 18'. Elytra olivaceous, slightly iridescent, legs ferruginous red, antennae piceous brown with three basal antennomeres reddish; lateral border of pronotum widened from anterior setigerous pore to posterior margin, narrowly flattened near basal angles, base punctate with deeper punctures near angles and along lateral margin; size 8.3 mm; Venezuela: Caracas *Adrimus affinis* Tschitschérine
- 19(16'). Smaller (5.5 mm); upper surface bronze with shiny green elytra, legs, palpi and basal antennomeres reddish; striae all well impressed, nearly smooth except inner striae very finely punctulate at base; intervals flattened on disc; Brazil: Pará *Adrimus aenescens* Tschitschérine
- 19'. Larger (6–7.5 mm) 20
- 20(19'). Upper surface metallic green, elytra lighter, legs and antennae dark, basal antennomeres and knees reddish; lateral border of pronotum narrow; lateral border of pronotum, apical part of elytral margin and suture yellowish-red; size 7–7.5 mm; Venezuela *Adrimus virens* Tschitschérine
- 20'. Upper surface piceous black, elytra with slight greenish iridescence, legs and antennae testaceous red; lateral border of pronotum reddish; elytra sericeous; pronotum very transverse, small, much narrower than elytra, base with a few coarse punctures, lateral margin flattened posteriorly; size 6–6.5 mm; Brazil 21
- 21(20'). Width of elytral intervals 4 and 6 subequal to adjacent intervals *Adrimus viridescens* (Bates)
- 21'. Elytral intervals 4 and 6 wider than adjacent intervals (probably only a variation of *A. viridescens* (Bates, 1872:177) *Adrimus geminatus* Bates

DESCRIPTIONS OF NEW SPECIES

In the descriptions the following characters common to all *Adrimus* are not repeated: two supraorbital setae on each side of head; lateral border of pronotum with two setae on each side, one in anterior half and one at hind angle; last abdominal sternum with one pair of setae in males, two pairs in females; hind tarsi with three basal tarsomeres sulcate on both sides; hind tarsi with basal tarsomere subequal in length to second and third tarsomeres combined. Information listed under the heading *Type Specimens* is verbatim label data except in three cases where bracketed interpolations have been added for clarity. Many specimens are damaged or missing parts. I have described the damage and noted the missing appendages of the holotypes to aid in recognizing them in the future.

Adrimus claripes, new species
(Fig. 9)

Type specimens.—*Holotype*, male (CMNH): Brazil, Alagoas, San Miguel dos Campos, IV.1984, F. M. Oliveira; *Allotype*, female (CS), two *paratypes*, females (CMNH), and one *paratype*, female (CS): same data as holotype. The holotype is missing seven antennomeres of the right antenna, the prothoracic and metathoracic right legs, and the mesothoracic left leg. Specimens examined: 5.

Diagnosis.—Group One species distinguished by very convex eyes; entirely pale legs; pronotum narrowed toward base with sides subsinuate before hind angles.

Description.—Length 7.5–8 mm (holotype 8 mm); greatest width 3.3–3.6 mm (holotype 3.3 mm). Upper surface black, lateral margin of pronotum reddish; legs, antennae and palpi ferrugineous, rather pale; underside dark brown.

Head (including eyes) as long as wide (1.5 mm); eyes very large and very convex (similar to Fig. 5); temples nearly disappeared; frontal impressions short, scarcely surpassing level of anterior supra-orbital seta; frons moderately convex, smooth. Antennae long, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 9) transverse, very convex behind the deep submarginal sulcus; basal impressions deep; space between impressions and basal angles irregularly depressed (the single male holotype) or moderately convex and smooth (remaining specimens, all female); space between impressions depressed and coarsely punctate; median impressed line deep.

Elytra oblong, convex; length 5 mm; greatest width 3.6 mm at $\frac{2}{3}$ length; basal border nearly straight toward very obtusely rounded humerus, obtusely joined to lateral border without angle; sides nearly straight and slightly divergent to greatest width, thence rounded to apex; preapical sinuosity faint; striae deep, very finely punctulate; intervals convex; dorsal puncture of third interval at mid-length.

Underside entirely impunctate, except metepisterna which are strongly punctate; metepisterna moderately narrowed posteriorly and less than 1.5 times longer than anterior width. Abdominal sterna with a depression on each side. Legs slender.

Etymology.—The name proposed for this species refers to its yellow-brown legs.

Adrimus latibasis, new species
(Fig. 10)

Type specimens.—*Holotype*, female (FMLT): Argentina, Salta Orán, Abra Grande 10.1–1.3.1963, R. Golbach. *Paratypes*, two (FMLT, CS), females: same data as holotype. All specimens immature and somewhat damaged. The holotype is missing the left antenna, seven antennomeres of the right antenna, all tarsi, and the right metathoracic leg. Specimens examined: 3.

Diagnosis.—Group One species distinguished by very convex eyes; legs, palpi, and antennomeres light ferrugineous; pronotum very transverse and very little narrowed toward base.

Description.—Length 8–8.8 mm (holotype 8.8 mm); greatest width 3.4–3.6 mm (holotype 3.6 mm). Upper surface blackish-brown; lateral margin of pronotum and elytra ferrugineous; basal antennomeres and legs light ferrugineous; underside and elytral epipleura light ferrugineous, probably from immaturity.

Head (including eyes) a little wider (1.6 mm) than long (1.5 mm); eyes very convex (similar to Fig. 5); temples disappeared; frontal impressions deep, elongate, reaching middle of eyes; frons very convex, smooth. Antennae thin, apical antennomeres missing in all specimens.

Pronotum (Fig. 10) transverse ($r_d = 0.69$), length 1.6 mm; moderately convex behind the thin submarginal sulcus; basal impressions short, deep, wide; space between impressions and basal angles convex; space between impressions slightly depressed with about ten scattered punctures on the inner side of impressions; hind angles square, not raised; median impressed line very deep and widened in middle.

Elytra oblong, moderately convex, short ($r_d = 1.39$), length 4.8 mm, greatest width 3.5 mm; basal border nearly straight to obtusely rounded humerus, joined to lateral margin without angle; sides

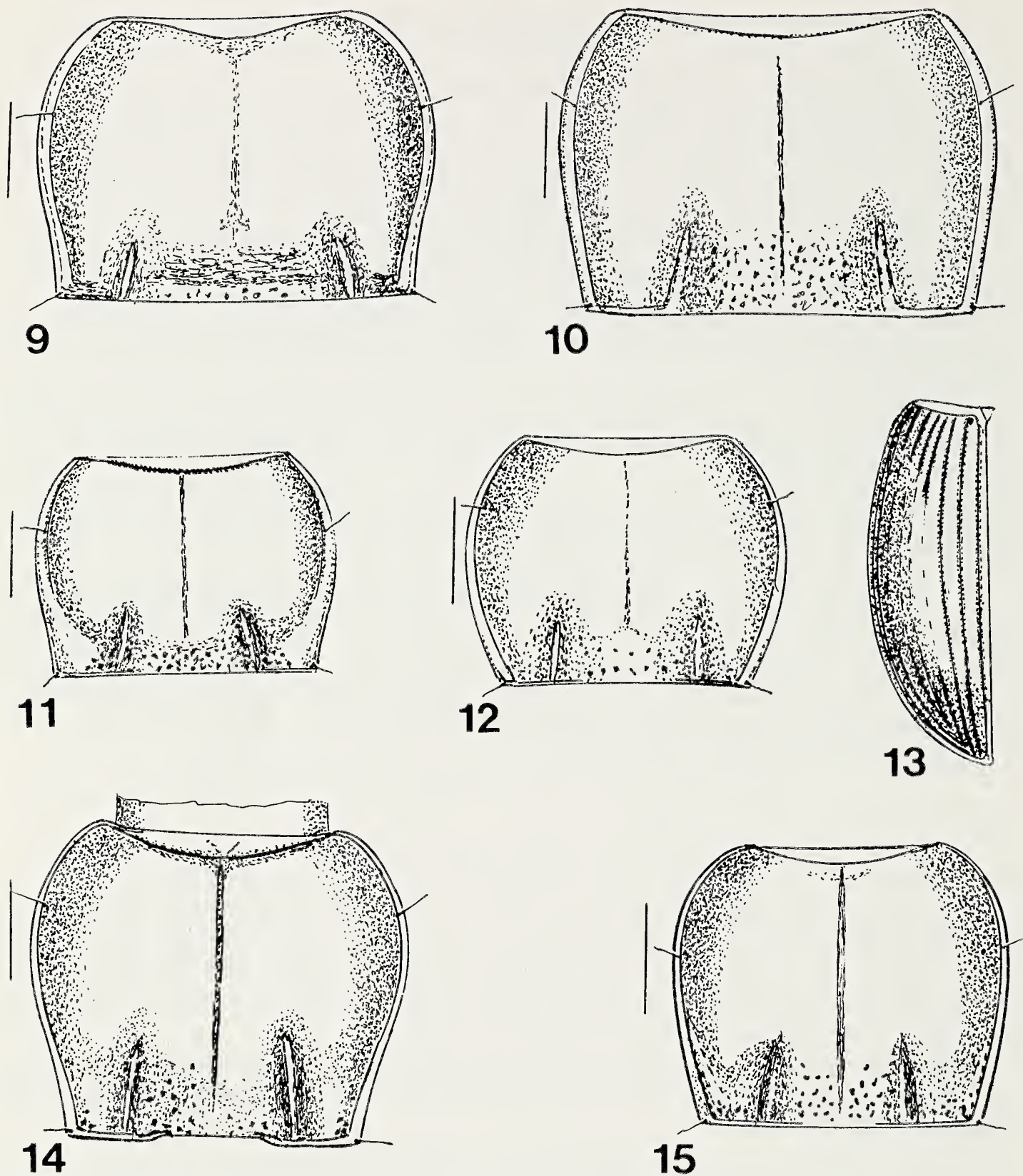


Fig. 9-15.—Pronota and elytra of *Adrimus*. 9, pronotum of *A. claripes*; 10, pronotum of *A. latibasis*; 11, pronotum of *A. suturalis*; 12, pronotum of *A. elytralis*; 13, left elytron of *A. elytralis*; 14, pronotum of *A. fuscipes*; 15, pronotum of *A. ventralis* (scale line = 1 mm).

nearly straight, subparallel; greatest width at $\frac{2}{3}$ length, thence rounded to apex; preapical sinuosity distinct; striae very deep, finely punctulate; all intervals convex; dorsal puncture of third interval slightly posterior to mid-length.

Underside impunctate except mesepisterna and metepisterna; metepisterna moderately narrowed posteriorly, 1.2 times longer than anterior width; abdominal sterna without depressed area on each side. Legs relatively robust.

Etymology.—The name proposed for this species refers to the wide base of the pronotum.

Adrimus suturalis, new species
(Fig. 11)

Type specimens.—*Holotype*, male (CMNH): Santarem Brazil, Acc. No. 2966. *Allotype*, female (CS) and *paratype*, female (CMNH): same data as holotype. The holotype is missing the tarsi of the left metathoracic leg. Specimens examined: 3.

Diagnosis.—Group One species distinguished by small pronotum with parallel sides subsinuate toward base; pronotal base ferrugineous; pronotal and elytral margins and posterior half of elytral suture red.

Description.—Length 6.1 mm; greatest width 2.4 mm. Upper surface blackish with lateral margins of pronotum and elytra, base of pronotum, apical half of elytral suture, apical margin and epipleura of elytra, antennae and palpi light ferrugineous; elytra more or less iridescent; underside black.

Head (including eyes) a little longer (1.2 mm) than wide (1.1 mm); eyes moderately convex (similar to Fig. 6), temples nearly disappeared; frontal impressions moderately deep, short, barely reaching level of antennal insertion; frons moderately convex, smooth. Antennae elongate, extending beyond pronotal base by three apical antennomeres.

Pronotum (Fig. 11) length 1.2 mm, transverse ($r_d = 0.75$), moderately convex behind deep submarginal sulcus; basal impressions deep, wide; space between impressions and basal angles slightly depressed and with a few punctures; space between impressions not depressed, irregularly punctate; hind angles not raised; median impressed line shallow.

Elytra oblong, slightly convex; length 3.6 mm; humeri obtusely rounded, basal and lateral borders joining at obtuse angle; sides slightly divergent to greatest width at $\frac{2}{3}$ length, thence obtusely rounded to apex; preapical sinuosity moderate; all striae deep and finely punctate; intervals moderately convex.

Underside entirely impunctate; metepisterna short, moderately narrowed behind; abdominal sterna with a moderate depression each side. Legs relatively slender.

Etymology.—The name proposed for this species was suggested by the ferrugineous elytral suture.

Adrimus elytralis, new species
(Fig. 12, 13)

Type specimen.—*Holotype*, female (CS); Bolivia, S.ta Cruz, Huflo de Chavez, Ascension, 500 m, 11–63. A single specimen, without name of collector, presented by J. Nègre. The holotype is damaged, only the first four antennomeres remaining of each antenna. Specimens examined: 1.

Diagnosis.—Group One species very easily recognized by small size and characteristic elytral striation (Fig. 13).

Description.—Length 6.3 mm; greatest width 2.5 mm. Head black, pronotum blackish, elytra black, very shiny, iridescent; lateral margin of pronotum and elytra reddish; four basal antennomeres (remainder lacking in only known specimen), palpi and elytral epipleura light ferrugineous; underside brown, abdomen a little lighter.

Head (including eyes) a little shorter than wide; eyes moderately convex (similar to Fig. 6), temples nearly disappeared; frontal impressions deep, short, not reaching level of anterior supraorbital setae; frons very convex, smooth.

Pronotum (Fig. 12); length 1.2 mm; transverse ($r_d = 0.75$); moderately convex behind deep submarginal sulcus; basal impressions wide, deep; space between impressions and basal angles nearly flat with a few punctures; space between impressions depressed, coarsely and sparsely punctate; hind angles somewhat raised; median impressed line moderately deep, nearly reaching base.

Elytra (Fig. 13) oblong, convex, especially posteriorly; length 3.6 mm; greatest width 2.5 mm; basal border slightly arcuate toward moderately rounded humeri, joined to lateral margin without angle; sides straight, moderately divergent to greatest width at $\frac{3}{5}$ length, thence obtusely rounded to apex; preapical sinuosity moderate; striae deep near base and apex, striae 3–8 very shallow in middle, finely punctate near base.

Underside impunctate; metepisterna wide and short, moderately narrowed posteriorly, 1.2 times longer than anterior width. Legs slender.

Etymology.—The name proposed for this species refers to the characteristic striation of the elytra.

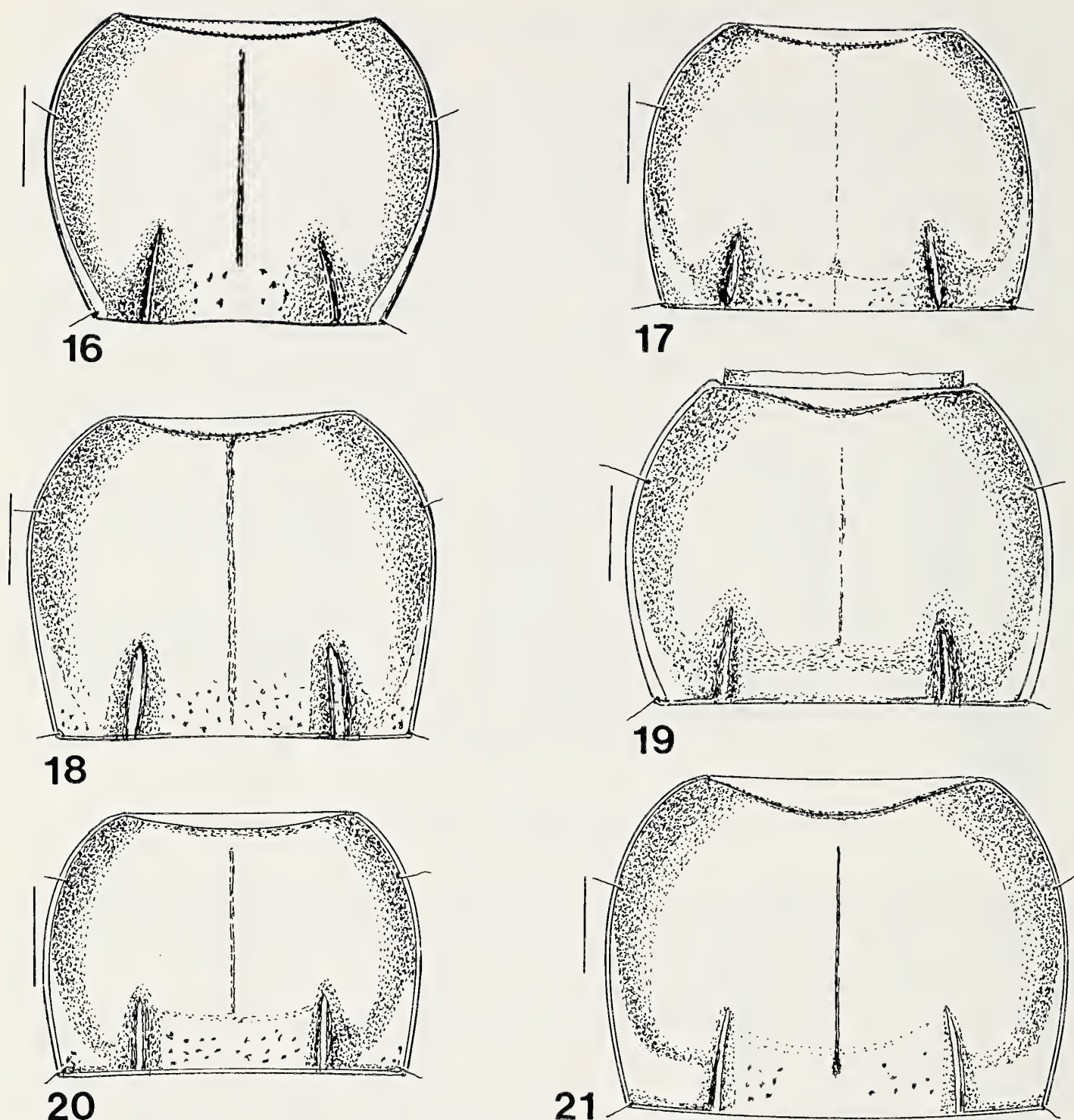


Fig. 16–21.—Pronota of *Adrimus*. 16, *A. balli*; 17, *A. proximus*; 18, *A. longior*; 19, *A. paulensis*; 20, *A. matoanus*; 21, *A. irideus* (scale line = 1 mm).

Adrimus ventralis, new species
(Fig. 15)

Type specimens.—*Holotype*, male (CMNH): Brazil, Alagoas, San Miguel dos Campos, IV. 1984, F. M. Oliveira. *Allotype*, female (CS), four *paratypes* (CMNH), and one *paratype* (CS): same data as holotype. The holotype is missing three antennomeres of the left antenna, the tarsi of the right mesothoracic leg, and the tibia and tarsi of the right metathoracic leg. Specimens examined: 7.

Diagnosis.—Group One species distinguished by moderately convex eyes; legs, three basal antennomeres, lateral border of pronotum, elytral epipleura and apex of abdomen ferrugineous; lateral elytral striae shallow at middle.

Description.—Length 6.8–7 mm (holotype 7 mm); greatest width 2.8–3 mm (holotype 2.9 mm). Head blackish; pronotum dark brown with ferrugineous lateral margins; elytra black, shiny, not iridescent, epipleura ferrugineous; antennae brown with three basal antennomeres lighter; legs ferrugineous; underside dark brown with apex of abdomen ferrugineous.

Head (including eyes) a little shorter (1.2 mm) than wide (1.4 mm); eyes moderately convex (similar to Fig. 6), temples very short; frontal impressions deep, very short, barely reaching level of antennal insertions; frons convex, smooth. Antennae elongate, extending beyond pronotal base by three apical antennomeres.

Pronotum (Fig. 15); length 1.3 mm; moderately transverse ($r_d = 0.68$); moderately convex behind submarginal sulcus; basal impressions wide, moderately deep; space between impressions and basal angles flattened at basal angles; space between impressions very little depressed and with a variable number of punctures (7–10 each side in most specimens); hind angles not raised; median impressed line wide, deep.

Elytra oblong, disc flat; length 4.4 mm; greatest width 3 mm; basal border rather strongly curved to moderately rounded humeri, joined to lateral margin without angle; sides very slightly arcuate, moderately divergent to greatest width at $\frac{2}{3}$ length, thence very obtusely rounded to apex; preapical sinuosity faint; striae 1–4 deep, remaining striae deep at base and apex, shallower in middle; striae nearly impunctate; all intervals convex.

Underside entirely impunctate; metepisterna short, barely longer than anterior width. Legs slender.

Etymology.—The name proposed for this species draws attention to the ferrugineous abdominal apex.

Adrimus balli, new species (Fig. 16)

Type specimens.—*Holotype*, male (UASM): Brazil, Pará, Belem, Mocambo, For. Reserve, Igapò for. Brasil Exp. 1978, G. E. & K. Ball collectors. *Allotype*, female (CS) and two *paratypes* (UASM): same data as holotype. The holotype is missing the left antenna, five antennomeres of the right antenna, and the left metathoracic leg. Specimens examined: 4.

Diagnosis.—Group One species distinguished by relatively stout body and large size, uniformly rounded pronotal sides, moderately transverse pronotum with basal angles slightly but obviously raised.

Description.—Length 8.2–8.5 mm (holotype 8.5 mm); greatest width 3.2 mm. Upper surface black, shiny, elytra with faint iridescence; legs reddish-brown; antennae brown with three basal antennomeres ferrugineous; underside brown, apical margin of last sternum a little lighter.

Head length 1.9 mm; width (including eyes) 1.5 mm; eyes moderately convex (similar to Fig. 6), temples about $\frac{1}{5}$ eye length; frontal impressions short, barely reaching level of antennal insertions; frons moderately convex, smooth. Antennae elongate, extending beyond pronotal base by four apical antennomeres.

Pronotum (Fig. 16); length 1.6 mm; moderately transverse ($r_d = 0.74$); moderately convex behind submarginal sulcus; basal impressions short, wide; space between impressions and hind angles convex, inclined toward hind angles which are obviously raised; space between impressions slightly depressed with a few small punctures; median impressed line moderately deep.

Elytra oblong, disc convex in middle; length 4.5 mm; greatest width 3.2 mm; basal border slightly curved toward obtusely rounded humeri, joined to lateral margin without angle; sides nearly straight, slightly divergent to greatest width at $\frac{2}{3}$ length, thence obtusely rounded to apex; preapical sinuosity moderate; striae deep, impunctate; all intervals convex.

Underside entirely impunctate; metepisterna moderately narrowed posteriorly, length 1.2 times anterior width; abdominal sterna smooth. Legs moderately slender.

Etymology.—It is with great pleasure that I dedicate this species to my friend Prof. George E. Ball.

Adrimus proximus, new species (Fig. 7, 17)

Type specimens.—*Holotype*, male (CMNH); Paraguay, Dept. Central, San Lorenzo, 23–24 Nov. 1986, John Kochalka, uv light. *Allotype*, female (CS), four

paratypes (CMNH) and one *paratype* (CS): same data as holotype. The holotype is missing two antennomeres of the left antenna. Specimens examined: 7.

Diagnosis.—Group One species distinguished by relatively flat eyes, elytral suture concolorous with rest of elytra, size 7.2–7.4 mm, legs brown, pronotum moderately narrowed posteriorly.

Description.—Length 7.2–7.4 mm (holotype 7.3 mm); greatest width 3 mm. Upper surface black, shiny, pronotum a little brownish with basal half of lateral border and hind angles ferrugineous; legs brown, tibiae and tarsi a little lighter; antennae dark brown with three basal antennomeres lighter; palpi ferrugineous; underside blackish-brown.

Head (including eyes) a little longer (1.4 mm) than wide (1.3 mm); eyes relatively flat, not very convex (Fig. 7), temples about $\frac{1}{2}$ eye length; frontal impressions moderately deep, short, barely reaching level of anterior margin of eyes; frons convex, smooth. Antennae elongate, extending beyond pronotal base by four apical antennomeres.

Pronotum (Fig. 17); length 1.5 mm; moderately transverse ($r_d = 0.72$); slightly convex behind moderately deep submarginal sulcus; basal impressions deep, extending to but shallower near basal angles; space between impressions and basal angles flattened; space between impressions moderately depressed, sparsely punctate; basal angles not raised; median impressed line shallow.

Elytra oblong, moderately convex; length 4.3 mm; greatest width 3 mm; basal border very slightly curved to obtusely rounded humeri, joined to lateral margin without angle; sides very slightly arcuate to greatest width at $\frac{2}{3}$ length, thence obtusely rounded to apex; preapical sinuosity very faint; striae deeply impressed and nearly impunctate.

Underside impunctate; metepisterna moderately narrowed posteriorly, length 1.2 times anterior width; abdominal sterna not or very slightly impressed on sides. Legs slender.

Etymology.—The name proposed for this species refers to its close resemblance to *A. uruguaicus* Tschitschérine.

Adrimus longior, new species

(Fig. 18)

Type specimens.—*Holotype*, male (CS): Brasilien, [Santa Catarina,] Nova Teutonia 27°11', 52°23' L, 3500 m, Fritz Plaumann. *Allotype*, female (CS), and *paratype*, male (CS): same data as holotype. The holotype is missing ten antennomeres of the right antenna and nine antennomeres of the left antenna. Specimens examined: 3.

Diagnosis.—Group One species distinguished by pronotal shape, with base punctate, narrow lateral border, and deep impunctate striae of elongate elytra.

Description.—Length 8.5–9.2 mm (holotype 9.2 mm); greatest width 3.3–3.5 mm (holotype 3.4 mm). Upper surface piceous-black, slightly shiny, elytra with a faint iridescence in some specimens; lateral margins of pronotum and elytra not reddish; legs brown, tarsi a little lighter; antennae brown with three basal antennomeres a little lighter; palpi ferrugineous; underside blackish.

Head (including eyes) as long as wide (1.6 mm); eyes moderately convex (similar to Fig. 6), temples nearly disappeared; frontal impressions moderately impressed, short, barely reaching level of anterior margin of eyes; frons moderately convex, smooth. Antennae elongate, extending beyond pronotal base by three apical antennomeres.

Pronotum (Fig. 18); length 1.7 mm; moderately transverse; slightly convex behind deep submarginal sulcus; basal impressions short; space between impressions and basal angles nearly flat, depressed at angles; space between impressions not depressed, with a few punctures; hind angles slightly raised; median impressed line moderately wide, deep on disc, very thin posteriorly, reaching base.

Elytra elongate, disc slightly convex, more convex at apex; length 5.1 mm, greatest width 3.5 mm; basal border moderately curved forward toward moderately rounded humeri, joined to lateral margin without angle; sides very little arcuate, nearly straight, slightly divergent to greatest width at $\frac{2}{3}$ length, thence strongly rounded to apex; preapical sinuosity very slight; striae deep, all equally impressed, not distinctly punctate.

Underside entirely impunctate, smooth; metepisterna narrowed posteriorly, length 1.5 times anterior width. Legs moderately slender.

Etymology.—The name proposed for this species refers to the relatively elongate elytra compared with closely allied species.

Adrimus paulensis, new species
(Fig. 19)

Type specimens.—*Holotype*, male (CS): [BRAZIL:] San Paulo Capital, Interlagos, Dr. Nick, 19.11.50. *Allotype*, female (CS): [BRAZIL:] San Paulo Capital, Sto Amaro, Dr. Nick, 21.9.54. The holotype is missing seven antennomeres of the right antenna and five antennomeres of the left antenna. Specimens examined: 3.

Diagnosis.—Group One species distinguished by pronotal shape, with sides uniformly arcuate, lateral border widened toward basal angles, base wholly impunctate.

Description.—Length 7.8–8.5 mm (holotype 8.4 mm); greatest width 3–3.2 mm (holotype 3 mm). Upper surface black with lateral margins of pronotum and elytra reddish; legs and antennae reddish brown, scape and palpi lighter; underside brown with elytral epipleura reddish.

Head (including eyes) a little longer than wide (1.5 mm); eyes moderately convex (similar to Fig. 6), temples very short; frontal impressions narrow, short, barely reaching level of anterior margin of eyes; frons rather convex, smooth. Antennae elongate, extending beyond pronotal base by three apical antennomeres.

Pronotum (Fig. 19); length 1.7 mm; transverse ($r_d = 0.71$), moderately convex behind very deep submarginal sulcus; basal impressions deep; space between impressions and basal angle nearly flat, inclined toward impressions; space between impressions depressed, impunctate; hind angles not raised; median impressed line narrow, moderately deep.

Elytra oblong, convex; length 5.5 mm; greatest width 3.2 mm; basal border curved toward very obtusely rounded humeri, joined to lateral border without angle; sides slightly arcuate to greatest width at $\frac{2}{3}$ length, thence rounded to apex; preapical sinuosity faint; striae deep, very finely punctulate.

Underside entirely impunctate; metepisterna moderately narrowed posteriorly, length 1.5 times anterior width; abdominal sterna not impressed at sides. Legs slender.

Variation.—A third specimen, labelled the same as the allotype, differs considerably from the two type specimens by its larger size and by having a row of punctures on the posterior half of the lateral border of the pronotum. It is probably a variant of this species. If not, it represents a new species.

Etymology.—The name proposed for this species refers to its provenance.

Adrimus matoanus, new species
(Fig. 20)

Type specimen.—*Holotype*, female (CMNH): Brazil, Mato Grosso, Diamantino, Fazienda Sao Joao, 6.II.1981, 450 m, Ekis & Young (white light). The holotype is missing the left antenna, the left prothoracic leg and all the right legs. Specimens examined: 1.

Diagnosis.—Group One species distinguished by small size, relatively flat pronotum and elytra; legs brown; antennae black, scape ferrugineous; outer elytral striae deep at base and apex, shallow in middle.

Description.—Length 6.7 mm; greatest width 2.7 mm. Upper surface black, shiny, not iridescent; legs and palpi brown; antennae black with scape ferrugineous; underside black, apex of last sternum brownish.

Head (including eyes) as long as wide; eyes wide and moderately convex (similar to Fig. 6), temples nearly disappeared; frontal impressions short, parallel, wide, barely reaching level of anterior margin of eyes; frons very convex, smooth. Antennae very thin, elongate, extending beyond pronotal base by three antennomeres.

Pronotum (Fig. 20); length 1.3 mm; transverse ($r_d = 0.68$); slightly convex behind submarginal sulcus; basal impressions deep, narrow; space between impressions and basal angles nearly flat; space between impressions depressed, slightly punctate; hind angles slightly raised; median impressed line very thin, shallow.

Elytra oblong, slightly convex; length 4.1 mm; greatest width 2.7 mm; basal border nearly straight toward obtusely rounded humeri, joined to lateral margins with an obtuse angle; sides nearly straight and very little divergent posteriorly to greatest width at $\frac{3}{4}$ length, thence rounded to apex; no preapical sinuosity; striae 1 and 2 deep, very finely punctulate at base; striae 3 deep in basal half; remaining striae moderately deep at base and apex, nearly effaced in middle.

Underside entirely impunctate; metepisterna moderately narrowed posteriorly, length 1.3 times anterior width; abdominal sterna not evidently depressed at sides. Legs moderately slender [some missing from only known specimen].

Etymology.—The name proposed for this species indicates its provenance.

***Adrimus irideus*, new species**
(Fig. 21)

Type specimens.—*Holotype*, male (CS): R[epublica]. A[rgentina]. Entre Rios, Parana Guazu, 22.6.54. *Allotype*, female (CS): same data as holotype. Both specimens with hand-written labels, without collector's name. Both specimens were presented to me by my late friend J. Nègre. The holotype is missing the right prothoracic leg and the left mesothoracic leg. Specimens examined: 2.

Diagnosis.—Group One species distinguished by wide general habitus; strong elytral iridescence; inner striae deep, outer striae shallower at middle; inner intervals convex, outer intervals flat at middle, deep depression in basal $\frac{1}{2}$ of elytra.

Description.—Length 7.5–8.3 mm (holotype 7.7 mm); greatest width 3.2–3.4 mm (holotype 3.2 mm). Upper surface black, shiny, elytra strongly iridescent; lateral margin of pronotum reddish before base; legs, antennae and palpi brown; underside brown.

Head (including eyes) as long as wide (1.6 mm); eyes moderately convex (similar to Fig. 6), temples nearly disappeared; frontal impressions wide, moderately deep, short, barely reaching level of anterior supraorbital seta; frons very convex, smooth. Antennae thin, elongate, extending beyond pronotal base by four apical antennomeres.

Pronotum (Fig. 21); length 1.65 mm; transverse ($r_d = 0.70$); convex behind very deep submarginal sulcus, much flatter in basal half; basal impressions deep, narrow; space between impressions and angles rather flat with a few superficial punctures; space between impressions slightly depressed with many scattered punctures; hind angles not raised; median impressed line narrow, moderately deep, not reaching base.

Elytra oblong, convex, with a deep depression at $\frac{1}{2}$ of length from base; length 5 mm; greatest width 3.4 mm; basal border slightly curved to humeri, joined to lateral margin without angle; sides slightly and uniformly arcuate to greatest width at mid-length, thence obtusely rounded to apex; preapical sinuosity very faint; striae 1–4 deep throughout, striae 5–7 always shallower except at base and apex; inner striae very finely punctulate in basal half; intervals 1–4 moderately convex, remaining intervals convex near base and apex, nearly flat at middle.

Underside smooth, impunctate; metepisterna elongate, strongly narrowed posteriorly, length more than 1.5 times anterior width; abdominal sterna depressed at sides. Legs slender.

Etymology.—The name proposed for this species refers to the strong iridescence of the elytra.

ACKNOWLEDGMENTS

My sincere thanks are due Prof. G. E. Ball, University of Alberta; Robert L. Davidson, Carnegie Museum of Natural History; and L. Terán, Fundación Miguel Lillo, Tucumán, for loans of the material that is the subject of this paper and for the generous donation of some duplicates for my collection. I am also grateful to Dr. Thierry Deuve, Ph. Bruneau de Miré and Dr. K. Desender for the loans of the types essential for the identification of *A. fuscipes* and *A. uruguaicus*. Moreover, I am particularly grateful to Robert L. Davidson for the revision of my manuscript.

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ERRATA

Vogt, R. C. 1993. Systematics of the false map turtles (*Graptemys pseudogeographica* complex: Reptilia, Testudines, Emydidae). *Annals of Carnegie Museum*, 61(1):1-46.

Fig. 10 (page 22) is incorrectly labeled: gel positions 1, 12, and 26 are *Chrysemys picta bellii*; gel positions 2, 4, 6, 8, 10, 13, 15, 17, 19, 21, 23, and 25 are *Graptemys ouachitensis*; gel positions 3, 5, 7, 9, 11, 14, 16, 18, 20, 22, and 24 are *Graptemys pseudogeographica*.

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RAUSCH, R. L. 1963. A review of the distribution of Holarctic mammals. Pp. 29–43, *in* Pacific Basin Biogeography (J. L. Gressitt, ed.), Bishop Museum Press, Honolulu, Hawaii, xx + 450 pp.
- 5) Unpublished dissertation:
SMITH, J. P. 1976. Review of Eocene mammals. Unpublished Ph.D. dissert., University of California, Berkeley, 302 pp.
- 6) Book:
WHITE, M. J. D. 1961. The Chromosomes. Methuen and Co., Ltd., London, 120 pp.
- 7) Journal articles with usual volume and issue number:
ANDERSON, W. I. 1969. Lower Mississippian condonts from northern Iowa. Journal of Paleontology, 43(4):916–928.

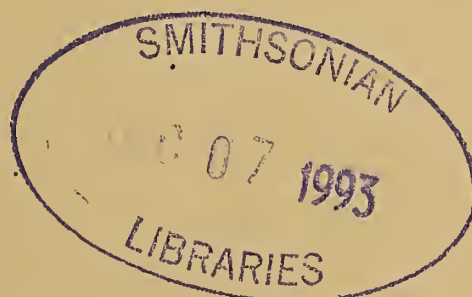
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CHENOPROSOPUS LEWISI, A NEW COCHLEOSAURID AMPHIBIAN
(AMPHIBIA: TEMNOSPONDYLI) FROM THE
PERMO-CARBONIFEROUS OF NORTH-CENTRAL TEXAS

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ABSTRACT

A unique specimen from the Permo-Carboniferous of north-central Texas represents a new species of cochleosaurid temnospondyl, *Chenoprosopus lewisi*, and the first occurrence of the genus outside the Lower Permian of New Mexico. The new material consists of a virtually complete skull with attached mandible and associated postcranial remains, including partial pectoral and pelvic girdles, femora, and a few vertebrae. Although the skull is only half the size of the smallest individual of the genoholotypic species *C. milleri*, the degree of ossification and development of dermal sculpture indicate an adult form. The genus is differentiated from other cochleosaurids by its more narrow and acuminate snout, little to no septomaxilla-lacrima contact, a jugal-lacrima contact that is equal to or shorter than the jugal-prefrontal contact, and a choana with a round anteromedial margin. Three derived characters unite the family Cochleosauridae: an elaborate jugal-pterygoid suture that excludes the maxilla and ectopterygoid from the subtemporal fossa, vomers that are elongated anterior to choanae, and choanae that are elongate and wide anteriorly. Despite similarities between *Chenoprosopus* and *Edops*, the conventional assignment of cochleosaurids to the Edopoidea is supported by only one derived character, an elongate premaxilla that borders a small, inset external naris. Archegosaurid temnospondyls resemble cochleosaurids in the possession of elongate premaxillae and vomers but lack small, posteriorly positioned external nares. If cochleosaurids and archegosaurids prove to be closely related, several characters regarded presently as derived for eryopoid-grade temnospondyls were developed independently from a cochleosaurid stock.

INTRODUCTION

The higher level taxonomy of the large and complex amphibian order Temnospondyli bears a strong historical influence of fossils from the Lower Permian of north-central Texas. More than half of the commonly recognized temnospondyl superfamilies (Trimerorhachoidea, Edopoidea, Dissorophioidea, and Eryopoidea), as well as many families within these groups, derive from Texas specimens. Cochleosaurids, however, have not been reported from this region despite their occurrence in the Lower Permian of New Mexico. A new species of the cochleosaurid *Chenoprosopus* is described here on the basis of a unique specimen discovered recently in Texas.

Within the Lower Permian of north-central Texas, the majority of tetrapod material has come from four "redbed" formations—the Archer City, Nocona, Petrolia, and Arroyo—that range in age from middle Wolfcampian (Asselian) to middle Leonardian (Artinskian). The new specimen, however, was found in the Markley Formation, a coal-bearing, terrigenous clastic unit that straddles the Virgilian–Wolfcampian (Carboniferous–Permian) boundary (DiMichele et al., 1991). Whereas vertebrate remains collected previously from this interval are few and fragmentary (Romer, 1935; Hook, 1989), the new specimen includes a virtually complete skull and several postcranial elements.

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The genus *Chenoprosopus* was established by Mehl (1913) on the basis of a partial skull collected near Arroyo de Agua, New Mexico, by Paul C. Miller. A second partial skull, also collected by Miller from the same deposit, was described briefly by Williston (1918). Although these specimens indicated an alligator-like skull of general temnospondyl design, the cochleosaurid affinities of *Chenoprosopus milleri* became clear only after two more-complete skulls were discovered in the Arroyo de Agua area (Langston, 1953). These four specimens are of intermediate size (approximate skull lengths range from 190 to 300 mm) and are from Lower Permian rocks that are said to Wolfcampian in age. Though well ossified, the new Texas specimen is only about half the size of the smallest skull from New Mexico.

Abbreviations used for collection repositories are: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; UCMP, University of California Museum of Paleontology, Berkeley; and USNM, National Museum of Natural History, Washington, D.C. Anatomical abbreviations used in the figures: a, angular; art, articular; c, clavicle; ct, cultriform process; d, dentary; dp, dermal plates; eo, exoccipital; f, frontal; fe, femur; i, interclavicle; ic, intercentrum; il, ilium; it, intertemporal; j, jugal; l, lacrimal; m, maxilla; m.f., Meckelian fenestra; n, nasal; na, neural arch; op, opisthotic; p, parietal; pal, palatine; pa.f., para-articular foramen; pf, postfrontal; pm, premaxilla; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; sm, septomaxilla; sp, splenial; spp, postsplenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer.

SYSTEMATIC PALEONTOLOGY

Class Amphibia

Order Temnospondyli

Superfamily Edopoidea

Family Cochleosauridae Broili *in* Zittel, 1923

Revised Diagnosis.—Primitive temnospondyl amphibians characterized by elongate antorbital region that consists mainly of elongate nasals, premaxillae, and vomers and that accommodates anterior palatal fossae and elongate, anteriorly widened choanae; no lateral lines; four-bone circumorbital series consisting of jugal, postorbital, postfrontal, and prefrontal; septomaxilla sculptured and included in skull roof; prefrontal triangular and elongate; intertemporal present; modest tabular horns; no squamosal contribution to supratympanic shelf; modest supratympanic flange; jugal-pterygoid contact excludes ectopterygoid and maxilla from subtemporal fossa; pterygoids contact cultriform process but do not meet anteriorly; premaxilla bears palatal buttress anteromedially inside marginal tooth row; pterygoid flange downturned ventrally and embays anteromedial part of subtemporal fossa; single elongate Meckelian fenestra; intercentra thin walled; interclavicle rhomboidal, reduced slightly, not elongated; iliac blade compressed laterally with little anteroposterior expansion and rudimentary posterodorsal process.

Chenoprosopus Mehl, 1913

Type Species.—*Chenoprosopus milleri* Mehl, 1913.

Revised Diagnosis.—Cochleosaurid temnospondyl distinguished from *Cochleosaurus* by more narrow and acuminate snout; pineal foramen closed in large or

adult individuals; no postparietal lappets; little to no septomaxilla-lacrimal contact; shorter jugal-lacrimal contact; maxillary teeth set closely, elongate, and slightly recurved; anteromedial margin of choana rounded; basal articulation sutured in large individuals; denticulated ridge directed posterolaterally from vomerine tusk site; and splenial contributes to mandibular symphysis.

Chenoprosopus lewisi, new species

Holotype.—USNM 437646, a nearly complete skull and associated postcranial elements. Collected in 1989 by Kenneth W. Craddock.

Type Locality, Stratigraphic Interval, and Age.—E. Robbins Survey, abstract 389, approximately 2 km west of Shannon, Clay County, Texas; UTM 14SNN66740346, Antelope 7.5' topographic quadrangle. Approximately 2.5 m below the base of informal sandstone member 13, Markley Formation, Bowie Group, of Hentz and Brown (1987); Pueblo Formation, Wichita Group, of Romer (1974). Virgilian-Wolfcampian boundary interval, Permo-Carboniferous.

Diagnosis.—Chenoprosopine cochleosaurid differentiated from *Chenoprosopus milleri* by appreciable contacts between maxilla and nasal and between postorbital and supratemporal, and by reduced vomerine tusks located at anteromedial margin of choana.

Etymology.—In honor of Arnold D. Lewis. Since his first trip to north-central Texas with the late Alfred S. Romer in 1954, Arnie's extraordinary collecting talents and preparation skills have enhanced greatly our knowledge of late Paleozoic vertebrates.

DESCRIPTION

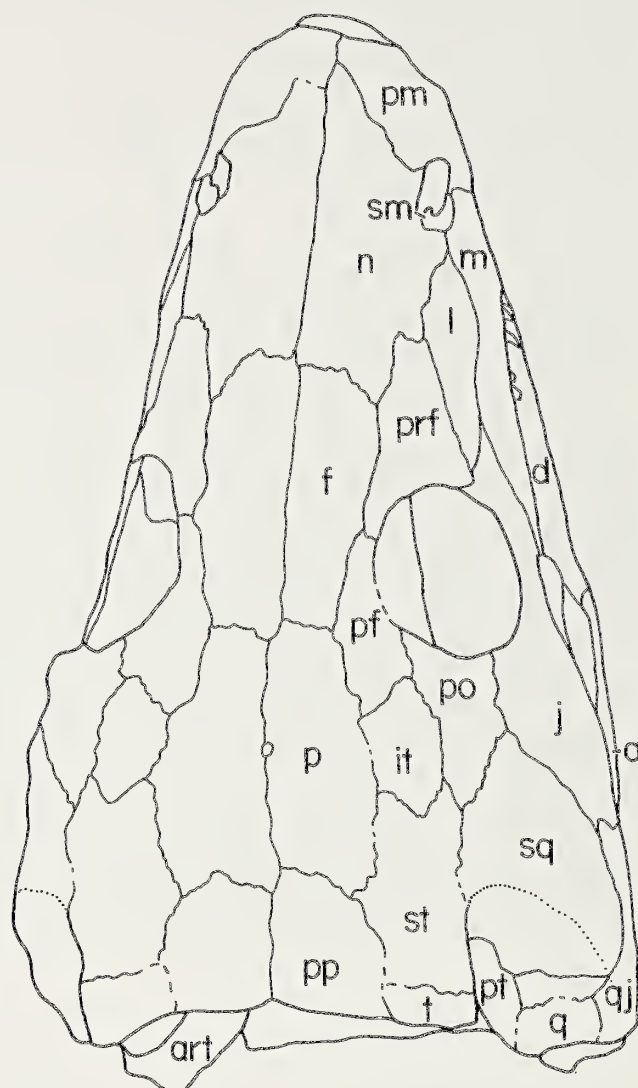
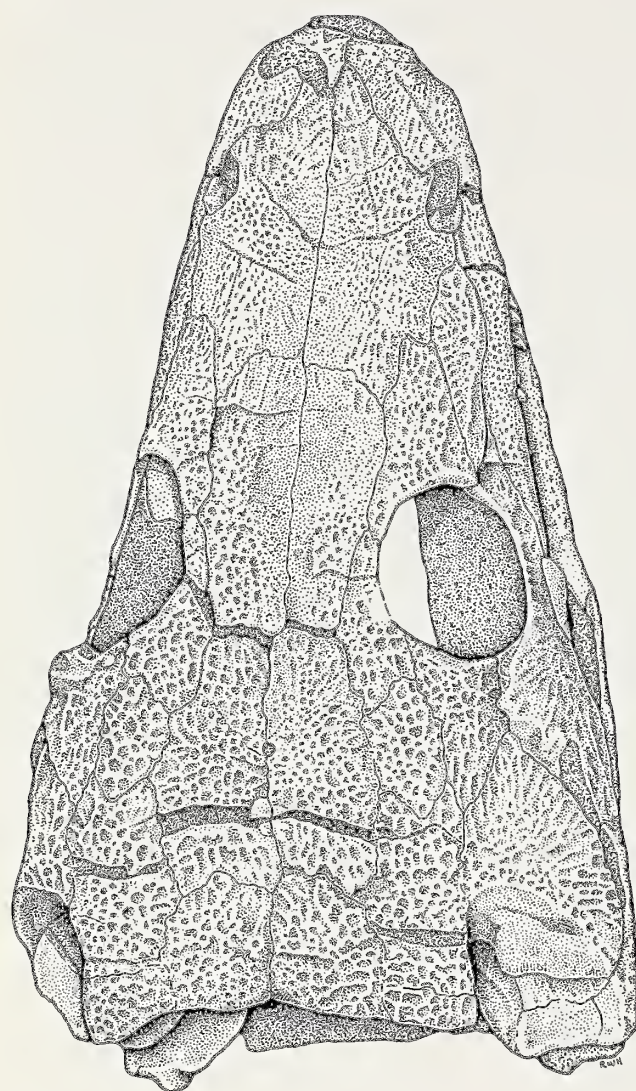
Skull

The skull shows little post-mortem disturbance and is nearly complete (Fig. 1, 2). In dorsal view, its outline is distinctly triangular, and the jaw articulation lies posterior to the level of the occiput. The otic notch is deep, open fully posteriorly, and bordered by the tabular, supratemporal, and squamosal. In the snout region, a median depression is flanked by longitudinal ridges that extend from the anteromedial margin of the orbits to the anterolateral portion of each nasal. The orbits are fairly large, circular, positioned midway along the skull length, and widely spaced. The slightly elongate external nares are situated close to the skull margin, where they open dorsolaterally. A small pineal foramen is present. In lateral view, a low profile is imparted by a gently rounded junction between the skull table and cheek region.

Despite the comparatively small size of the skull, the degree of ossification and the development of dermal sculpture indicate that the specimen may be regarded as adult. A sculpture of subcircular pits, considered as a mature condition in eryopoids (Boy, 1988, 1989, 1990) and other temnospondyls, predominates on the skull table and orbital margins. Areas of ridge-and-groove ornament indicative of intensive growth zones (Bystrow, 1935) are developed chiefly on the snout and cheeks. As in *Chenoprosopus milleri*, *Cochleosaurus*, and *Macrerpeton* [*Mytaras*], dermal sculpture is subdued within the antorbital depression. No lateral lines are developed.

Although the tip of the snout is missing, the intact and attached mandibular symphysis indicates that only a minor portion of each premaxilla has been lost. A small triangular piece of bone preserved on the left side of the longitudinal

A



1 cm

B

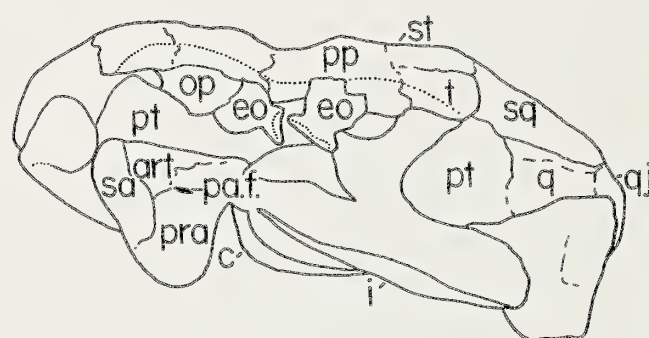
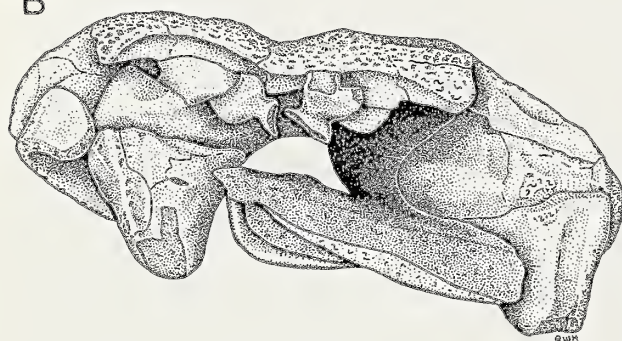


Fig. 1.—*Chenoprosopus lewisi*, holotype, USNM 437646. A, dorsal view. B, occipital view.

midline appears to be part of the left premaxilla rather than a discrete internasal ossification; by either interpretation, the median configuration of the premaxillae and nasals is asymmetrical. The premaxilla-nasal suture extends posterolaterally from the dorsal midline to the external naris, where the premaxilla forms the anterior margin of the narial opening.

The bases of six successive labyrinthine teeth are preserved on the left premaxilla. They are of uniform size, with a basal diameter approximately one-third

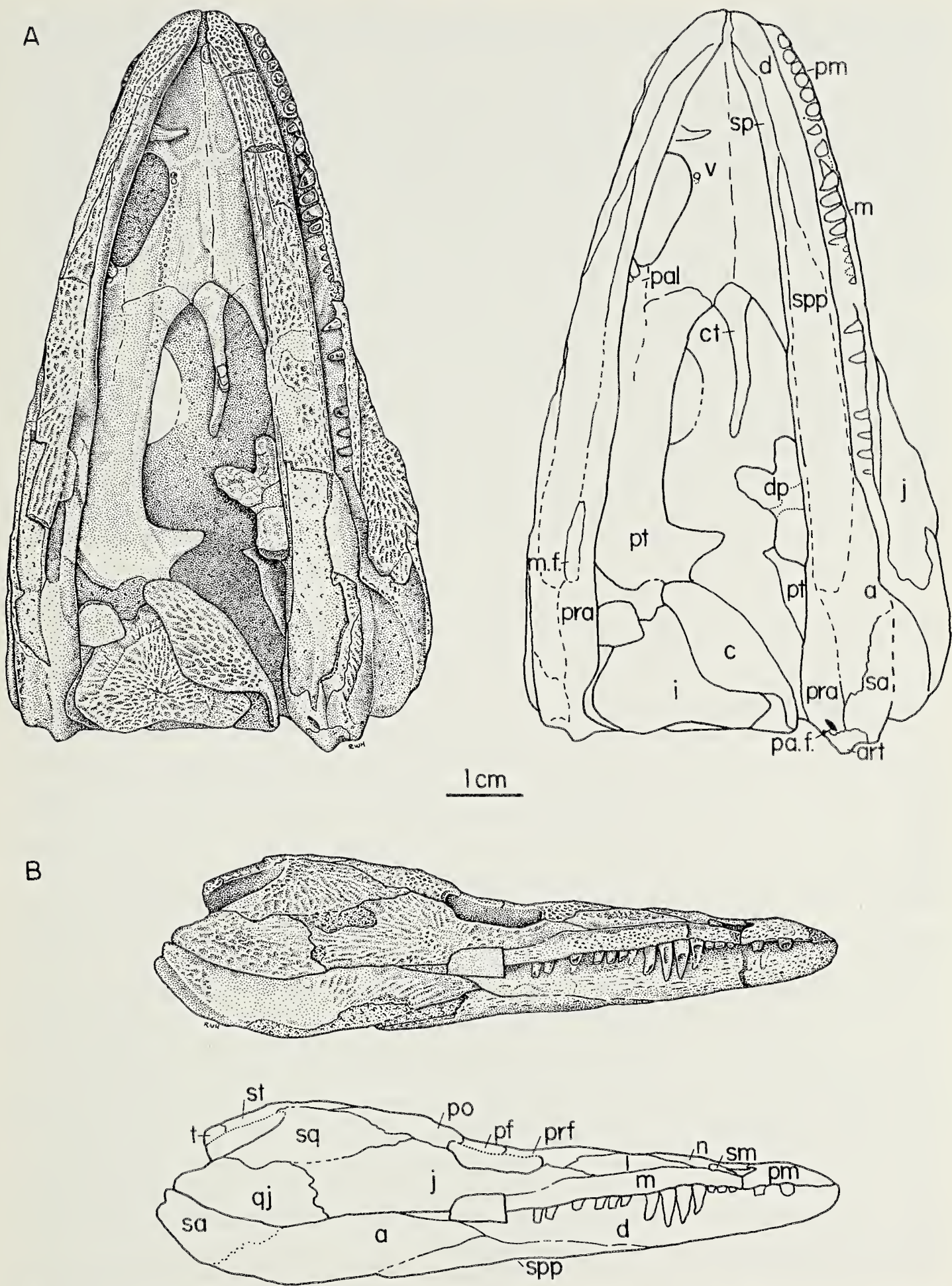


Fig. 2.—*Chenoprosopus lewisi*, holotype, USNM 437646. A, ventral view. B, right lateral view; angular-surangular suture is based on left mandibular ramus.

larger than that of the anteriormost maxillary tooth. Because both premaxillae are incomplete anteriorly, a reasonable estimate of total tooth positions is not possible.

Below the naris, the premaxilla has a short contact with the maxilla at the skull margin. The maxilla is excluded from the narial opening by the septomaxilla. The preorbital portion of the maxilla is swollen slightly. At the level of the anterior margin of the orbit, the height of the maxilla decreases abruptly by half, and the element tapers posteriorly to a termination below the jugal before reaching the quadratojugal. A short maxilla-nasal suture is evident on both sides of the skull, followed by contacts with the lacrimal and jugal.

The bases of the maxillary teeth are apposed closely to the external margin of the maxilla. A minimum of 34 maxillary tooth positions is estimated. Many teeth are incomplete, but virtually all of the first 11 or 12 alveoli appear to have been occupied simultaneously. Although the first two maxillary teeth are smaller than those of the adjacent portion of the premaxillary dentition, tooth size increases abruptly such that the largest teeth occupy sites three through seven. These teeth have relatively narrow, round bases, recurved distal halves, and sharply pointed ends. Following an approximately 50 percent decrease in height at about position eight, tooth size again increases slightly at position nine before diminishing gradually along the tooth row.

Both septomaxillae are preserved essentially in place between the maxillae and nasals. The delicately pitted posterior section of this small element is a very minor part of the skull roof. A process arising from the medial side extends anterolaterally into the posterior portion of the narial opening, and a larger lateral flange forms the posteroventral margin of the naris.

Paired nasals and frontals are the major components of the midline series. The expansive, transversely convex nasal forms the dorsomedial margin of the naris and contacts the maxilla, lacrimal, and prefrontal posterolaterally. The nasal-frontal suture trends anteromedially towards the longitudinal midline, where the opposing nasals share an extensive suture that equals nearly a third of the entire skull length. Almost all of the interorbital region is formed by the rectangular frontals. The lateral boundary of each is joined equally by the prefrontal and postfrontal. Posteriorly, the frontals overlap the parietals along a fairly straight suture.

A circumorbital series of four bones is present. The triangular prefrontal, which forms the anteromedial quarter of the orbital margin, is bounded laterally by the lacrimal and jugal and medially by the nasal and frontal; it has brief contact with the postfrontal between the frontal and the medial rim of the orbit. Both the postfrontal and postorbital are tapered posteriorly and form a grossly interdigitated union with adjacent elements of the skull table and cheek. The jugal alone encloses the lateral portion of the orbit. A brief jugal-prefrontal contact excludes the lacrimal from the orbital margin. Posterolateral to the orbit, the jugal expands to form a major part of the cheek; it also forms a minor fraction of the skull margin between the maxilla and the quadratojugal.

The skull table is of a primitive design with long supratemporal-postparietal contacts and large intertemporals. Most of the sutures are sinuous and a few are difficult to trace. The pineal foramen is small and flush with the skull surface. From its anterior junction with the frontal, the parietal is contacted laterally by the postfrontal, intertemporal, and supratemporal, and posteriorly by the post-

parietal. The postparietal is slightly longer than wide and is depressed towards the midline. There is no development of the pedal-shaped postparietal lappets that characterize comparably sized specimens of *Cochleosaurus*.

Together with the adjoining tabulars, the paired postparietals form the posterior margin of the skull table. In occipital view (Fig. 1B), a posteriorly directed dorsal shelf is developed on the postparietals and diminishes laterally onto the tabulars. Below and perpendicular to this shelf, the postparietal consists of an unsculptured vertical flange that contacted the exoccipital medially and perhaps the paroccipital process laterally. A similar flange on the underside of the tabular clearly received the paroccipital process. Though the right tabular is incomplete, the posterolateral corner of the left tabular is bluntly acuminate and moderately downturned.

All of the lateral margin of the tabular and approximately half of the supratemporal border the otic notch. A dorsal shelf comparable to that of the occiput is formed by these elements and overhangs an unsculptured vertical flange of modest size; in descriptions of the dissorophoid otic notch (Bolt, 1974), these two structures have been termed the supratympanic shelf and supratympanic flange. The courses of supratemporal-tabular and supratemporal-squamosal sutures on the flange cannot be determined with certainty. In front of the notch, the supratemporal joins the squamosal. Medial to a brief supratemporal-postorbital contact, the suture between the supratemporal and intertemporal forms a posteriorly directed V.

The posterior cheek region consists of the jugal, squamosal, and quadratojugal. As the largest of these elements, the squamosal adjoins the postorbital and supratemporal medially and comprises the anterolateral portion of the otic notch, which is not sculptured; although this thin, unsculptured portion is disrupted on the left side of the skull and incomplete on the right side, it appears to have overlapped both the pterygoid and quadrate within the otic notch. Laterally, the squamosal is bounded by the jugal and quadratojugal. In lateral view (Fig. 2B), the convex lateral margin of the quadratojugal extends slightly below the jaw articulation.

The quadrate forms the posteroventral portion of the otic notch and suspensorium. A rudimentary dorsal process is preserved on the posteromedial portion of the right quadrate; a similar boss is present in a more-damaged condition on the right quadrate of UCMP 33439. Although this projection may be homologous to the dorsal quadrate process of dissorophoids (Bolt and Lombard, 1985), imperfect preservation precludes anything beyond topologic comparisons. Medial to this process, the quadrate is joined by the pterygoid.

Description of the palate is hindered by the mandible, which is attached and obscures most of the marginal elements. I have employed a variety of preparation techniques in an effort to delimit palatal sutures, but most contacts cannot be traced. In general structure, however, the palate is very similar to that of *Chenoprosopus milleri* as described by Langston (1953).

The most striking palatal feature is an elongate choana that nearly reaches the level of the anterior limit of the interpterygoid vacuities (Fig. 2A). Although the lateral margin of the choana is not exposed, the opening lacks the anterior expansion and triangular shape that characterizes *Cochleosaurus*. Anterior palatal fossae occur on the vomers as modest concavities separated by a thin longitudinal septum; the fossae may be formed in part by the premaxillae, but no vomer-premaxilla suture can be determined. The length of each interpterygoid vacuity

is approximately three times greater than its width, or equal to about a third of the skull length. From their anterior closure against the cultriform process, the vacuities widen and become broadly rounded near the level of the basal process.

A small, poorly preserved vomerine tusk and replacement pit occupy a small platform near the anteromedial margin of the choana. In contrast to *C. milleri*, in which the vomerine tusks are larger and placed in a more lateral position, the condition of *C. lewisi* resembles that of *Cochleosaurus*. A large, detached tooth at the anterior end of the right choana is interpreted as a displaced dentary tooth. At the posterolateral margin of the choana, a second palatal tusk is present on the palatine and is accompanied by a replacement pit; the basal diameter of this tusk is slightly greater than that of the largest maxillary tooth. A probable ectopterygoid tusk cannot be observed because of the obstructing mandible. As in *C. milleri*, a denticulated ridge extends posterolaterally from the anteromedial margin of the choana to the anterior third of the interpterygoid vacuity, and much of the pterygoid is covered by smaller denticles.

The medial edge of the palatal ramus of the pterygoid is thickened along the margin of the interpterygoid vacuity. This feature merges anteriorly with the denticle-bearing ridge of the vomer described above. The relationships between the pterygoids, vomers, and cultriform process appear to be the same as *C. milleri*: a very brief pterygoid-cultriform contact closes the anterior portion of each interpterygoid vacuity, and the pterygoids do not meet anteriorly along the midline. Like most other cochleosaurids, however, the anteromedial termination of the pterygoids is very difficult to interpret. The basal process of the pterygoid is triangular, as in *Cochleosaurus florensis* (Godfrey and Holmes, in press), and apparently not sutured to the parasphenoid, which is not preserved in USNM 437646. At the level of the basal articulation, a posterolaterally directed, slightly downturned flange arises from the palatal ramus to embay the anteromedial portion of the subtemporal fossa. On the medial surface of the vertically oriented quadrate ramus of the right pterygoid, a modest horizontal shelf may represent the posterior portion of the excavatio tympanica. A shorter, deeper recess is present along the same plane just anterior to the posteromedial end of the pterygoid.

The parasphenoid is represented only by the anterior half of the cultriform process. The sphenethmoid, the main parasphenoidal body, and the basisphenoid are absent.

The articular surface of the quadrate is not exposed. Judging from the left articular and right quadrate, which can be seen in dorsal and posterior views respectively, the transverse axis of articulation has a modest anteromedial orientation, and the medial condyle is slightly lower than the smaller lateral condyle. The quadratojugal appears to have contributed to the lateral condylar facet.

A small portion of the epipterygoid may be preserved on the right side of the skull. Here, within the otic notch, the thin posteroventral part of the squamosal appears to have been lost along a transverse break. If identified correctly, the epipterygoid was extensively ossified.

As shown by Fig. 1B, the occipital portion of the braincase is disrupted and incomplete. Because the posterior part of the skull roof is collapsed and the exoccipitals are displaced, the exact nature of the posttemporal fossae cannot be determined. On the basis of the left side of the occiput, however, the fossa appears to have been small and enclosed entirely by the exoccipital, paroccipital process, and postparietal. The exoccipital is attached to the postparietal by a stout ascending process. Below a constriction that flanked the foramen magnum, each

exoccipital expands to contribute a crescent-shaped condyle that would have formed about a third of the occipital condyle. The basioccipital is not present. The left paroccipital process, which appears to be in place, has a broad contact with the occipital flange of the tabular and postparietal.

Lower Jaw

The lower jaw of USNM 437646 differs little from those of *Chenoprosopus milleri*, *Cochleosaurus*, or *Macrerpeton* [*Mytaras*]. Several areas cannot be described, however, because both rami are inextricably closed in a near lifelike position. Both dentary tooth rows, the coronoids, and the adductor fossae are obscured. The posteromedial portion of the right ramus is covered by the partial pectoral girdle, and weathering of the deepest part of each ramus has left only impressions of internal bone surfaces (Fig. 2).

Dermal sculpture similar to that of the skull is developed on the lateral and ventral portions of the jaw. Whereas most of the dentary and postsplenial bear a pitted pattern, the angular and surangular are dominated by ridge-and-groove ornament. No lateral line sulci are present; those described with reservation by Langston (1953) in *C. milleri* are only dermal sculpture.

From the dorsoventrally low symphyseal region, the depth of the lower jaw increases to a maximum at the level of the anterior part of the adductor fossa. Although the dorsal surface of the mandible cannot be observed, the jaw articulation appears to be elevated slightly above the tooth row. A broad groove is developed on the posteroventral face of the articular region. On the medial surface below the anterior portion of the adductor fossa, a single elongate Meckelian fenestra is enclosed by the prearticular and postsplenial; the articular may form the posterior margin of this opening as in *Cochleosaurus florensis* (Godfrey and Holmes, in press) and *Chenoprosopus milleri*, but contacts cannot be determined with certainty in this region. An oval para-articular foramen is present adjacent to the articular-prearticular contact on the posteromedial surface of the prearticular.

Even though both postsplenials are incomplete, they clearly are elongate elements that form nearly two-thirds of the ventral portion of each ramus. Examination of UCMP 33439 shows that the postsplenial ("angular" of Langston, 1953) of *C. milleri* also is a major element, extending for approximately half the length of the mandible. In both species, the postsplenial ends posteriorly at the level of the posterior end of the Meckelian fenestra. In contrast to the relatively simple sutures between the dentary, splenial, postsplenial, angular, and prearticular, the angular-surangular suture is strongly interdigitated on the lateral surface of the mandible. The surangular joins the prearticular along the upturned posteroventral portion of the lower jaw and terminates against the articular before reaching the medial surface.

Displacement of the suspensorium region on the left side of the skull reveals much of the glenoid fossa of the left articular. The fossa is oriented anteromedially and is divided into lateral and medial facets by a subtle ridge; the medial facet is depressed relative to lateral facet. A small retroarticular process merges ventrally with the ridge that forms the inner margin of the articular groove noted above.

Postcranial Skeleton

A significant portion of the pectoral girdle is preserved in association with the skull. Additional postcranial elements have been removed from or left on the

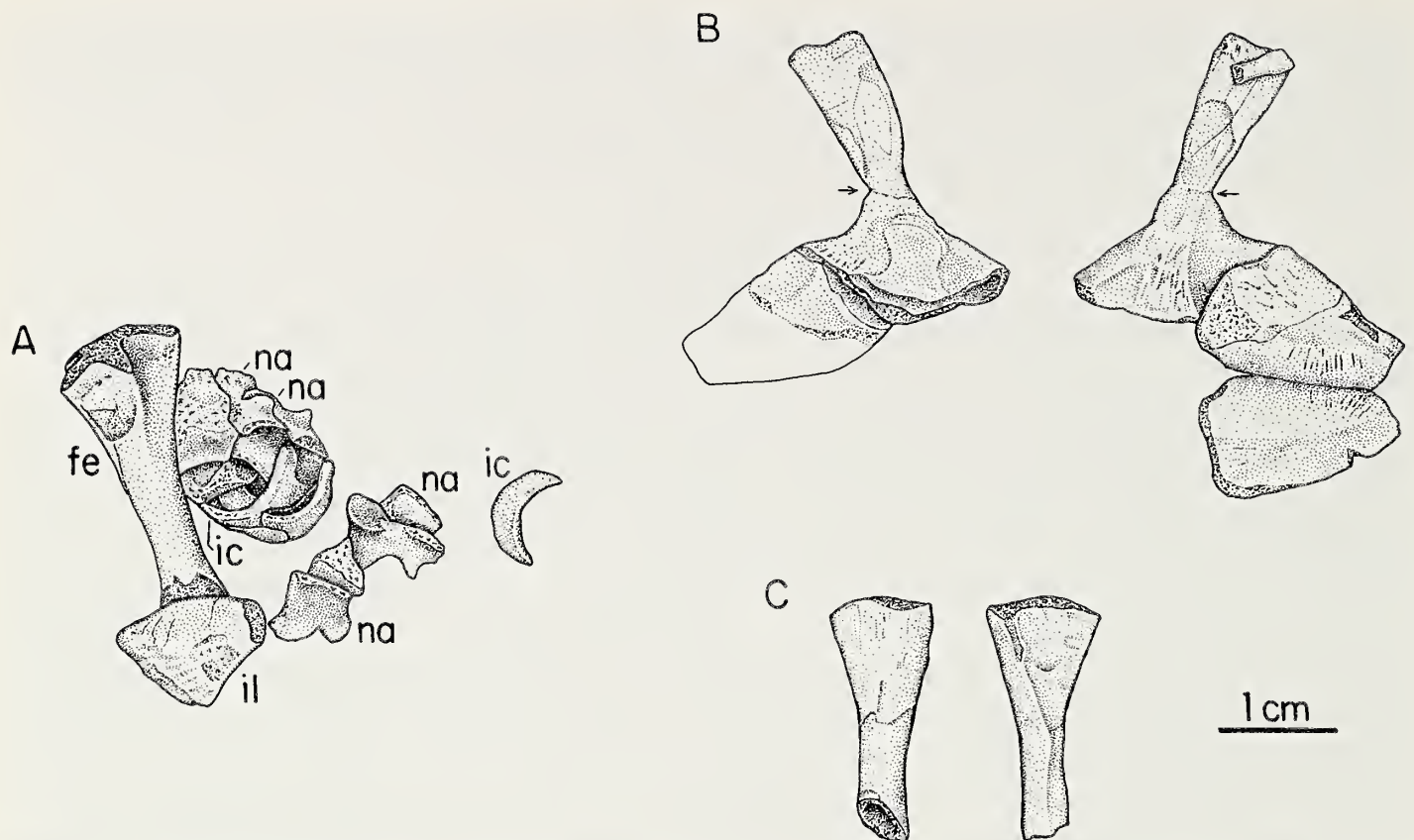


Fig. 3.—*Chenoprosopus lewisi*, holotype, USNM 437646. A, partial left femur in posterodorsal view, partial left ilium in medial view, and vertebral remains as preserved in coprolitic association. B, left, right ilium and ischium in lateral view (unshaded area covered by matrix); right, right ilium and ischium, and left ischium in medial view (arrow indicates position of break on ilium). C, proximal half of right femur in dorsal and ventral views.

surface of an approximately 60 mm-long spiral coprolite that was found next to the skull. To my knowledge, these are the only postcranial remains that can be attributed to *Chenoprosopus* with certainty. A Texas specimen mentioned by Romer (1947) in conjunction with *C. milleri* was found to pertain to another genus upon full preparation (W. Langston, personal communication). Although the material described below is limited, it resembles the few postcranial elements of *Cochleosaurus* that have been illustrated or described (Steen, 1938; Klembara, 1985).

Several vertebral elements are exposed partially in a mostly jumbled and damaged state on or adjacent to the coprolite (Fig. 3A). Four neural arches are present, two of which are in articulation. The absence of well-defined transverse processes suggests that these represent caudal vertebrae, but no hemal spines accompany the intercentra. Without additional data on cochleosaurid vertebrae, I cannot assign these remains to a specific part of the column. As preserved, the neural spines are short and unornamented. The anterior and posterior zygapophyses are nearly on the same horizontal plane, and they appear to be inclined only little. Below the anterior zygapophysis, the pedicle projects ventrolaterally and, where preserved in three neural arches, terminates in an anteroposteriorly broad, unfinished, ventrolaterally facing surface. The central elements are crescent-shaped and are presumed to be intercentra. They are not thickened internally and consist mainly of finished bone externally. Such thin-walled construction is found also in the vertebrae of *Dendrerpeton* (Carroll, 1967). No rib facets are present.

The anterior half of the interclavicle is exposed in ventral view and is partially

underlapped by the left clavicle (Fig. 1, 2A). An unsculptured bone preserved adjacent to the right side of the interclavicle cannot be identified. Ridge-and-groove ornamentation is the predominant sculpture on the external surface of both the interclavicle and clavicle. The width of the interclavicle is greatest at the level of its ossification center; half this width equals the anterior length of the element, as well as the greatest width of the clavicle. This suggests a rhombic interclavicle, as found in *Macrerpeton* [*Mytaras*] and *Cochleosaurus* (Steen, 1931, 1938). Most of the clavicular facet is intact on the right side, which indicates a relatively modest overlap between the interclavicle and clavicles. The clavicle is of typical design, consisting of a vertical cleithral process that arises from the posterolateral corner of the horizontally flat ventral plate.

With the exception of the pubis, the pelvic girdle is well represented. The lower half of the left ilium overlies the proximal portion of the left femur but cannot be removed without damaging both elements (Fig. 3A). As depicted in Fig. 3B, the detached right iliac blade has been restored to the main body of the right ilium. The acetabular area is defined sharply and is associated with a dorsal buttress typical of primitive tetrapods. Anterior to the acetabulum, the ilium turns laterally to form a flat anterior face that expands ventrally. Above the supra-acetabular buttress, the ilium continues as a simple blade that is oriented dorso-posteriorly in lateral perspective and recurved medially if viewed anteriorly or posteriorly. There is a very slight anteroposterior expansion beyond the "neck," but nothing comparable to that of roughly contemporaneous temnospondyls (*Eryops*, *Parioxys*, *Edops*, or various dissorophids). In medial view, a posteroventral concavity is defined by a curved ridge that extends from the midpoint of the ventral margin to the posterior edge of the iliac blade. Anterior to this ridge, the ilium is striated and thickened. The end of the iliac blade may be incomplete as preserved, and the area of a possible ilio-sacral attachment is covered by a bone fragment; though the latter may be a rib, it is too small for a sacral rib.

A simple iliac blade with little anteroposterior expansion has been interpreted as a juvenile condition in primitive temnospondyls on the basis of the diminutive *Eugyrinus* and several ilia attributed to *Dendrerpeton* (Milner, 1980b). Although this may be true, the ilium described here for *Chenoprosopus* compares favorably with significantly larger ilia from Florence that Klembara (1985) attributed to *Cochleosaurus*, as well as the largest known ilia of *Amphibamus lyelli*, an Upper Carboniferous dissorophoid from Linton, Ohio (Hook and Baird, 1984). A partial ilium assigned to *Edops* (Romer and Witter, 1942) differs in that it shows considerable expansion above the acetabulum.

The ischia are preserved in a flattened manner such that they contact each other along their ventral margins. Both are exposed fully in medial view, but only the anterior portion of the external surfaces has been prepared. The bone is thin except where it swells to enclose the posteroventral portion of the acetabulum, which is bordered by a pronounced ridge. Posterior to the acetabular area, the external surface of the ischium is concave and faces ventrolaterally. A roughened symphyseal contact between the ischia is not apparent; rather, the posteroventral portion of the internal face is striated vertically to suggest a ligamentous attachment.

Most of the left femur is preserved on the coprolite, but the proximal end is detached and its position is occupied by the incomplete left ilium (Fig. 3A). The proximal half of the right femur was prepared free of matrix (Fig. 3C). Based

primarily on the nearly complete left femur, a length of 29 mm is estimated. Both ends are unfinished, and the lateral face of the posterior distal condyle is collapsed inward. Because the outermost part of the posterior condyle has been lost to weathering, the anterior condyle appears to extend more distally. In dorsal view, the anterior or medial surface of the femur is markedly concave, and both ends expand to almost three times the width of the shaft. The anterior and posterior distal condyles are divided by a well-defined intercondylar fossa. Viewed end-on, the proximal end resembles an asymmetric D. This unfinished area merges anteroventrally with the unossified tip of the internal trochanter. Although the area of the fourth trochanter is damaged and cannot be assessed, the adductor crest clearly is a continuation of the ridge that accommodates the internal trochanter. The crest is a sharp, anteroposteriorly trending ventral ridge that is developed most strongly on the proximal to middle portion of the shaft. On the posteriorly exposed part of the left femur, the crest appears to diminish distally and merge with the medial boundary of the popliteal space. The incomplete nature of the distal end of the femur precludes any recognition of discrete articular surfaces.

Dermal Ossifications

A. D. Lewis, who skillfully prepared the skull, reports that much of the intermandibular area was occupied by scales. Several of these remain attached to the left mandibular ramus and the cultriform process (Fig. 2A). Though they are preserved infrequently and not likely to survive mechanical preparation, similar ossifications are found in other Permo-Carboniferous amphibians. Many oat-shaped scales contained in the coprolitic mass were not salvaged because of their intimate association with more significant postcranial elements.

DISCUSSION

Characteristics and Species of Chenoprosopus

The great size difference between the unique specimen of *Chenoprosopus lewisi* and all specimens of *C. milleri* makes generic definition somewhat difficult and specific differentiation suspect. To a lesser extent, similar problems exist among *Cochleosaurus bohemicus* (represented by a large sample from Nýřany, Czechoslovakia, that encompasses considerable size variation: Steen, 1938; Milner, 1980a), *Cochleosaurus florensis* (known from three skulls of small to intermediate size from Florence, Nova Scotia: Rieppel, 1980; Godfrey and Holmes, in press), and an unnamed species of *Cochleosaurus* from Linton, Ohio (known from two incomplete skulls of intermediate size: "*Leptophractus*" of various authors, "*Gaudrya*" of Hook and Baird, 1986). Pending the completion of a redescription of *C. bohemicus* by S. E. K. Sequeira, I have relied on growth trends in European eryopoids (Meyer, 1858; Boy, 1988, 1989, 1990) to judge what variations may be size-related in cochleosaurids.

Chenoprosopus is distinguished by a suite of characters that are presented above in the diagnoses of the genus and the family to which it belongs, the Cochleosauridae. Among these features are several shared derived characters that serve to differentiate the genus from *Cochleosaurus* and other primitive temnospondyls: (1) snout more narrow and acuminate than in comparably sized specimens of *Cochleosaurus*, *Macrerpeton*, and *Parioxys*; (2) little to no septomaxilla-lacrimal contact (discussed below); (3) length of jugal-lacrimal contact equal to or, with

size increase, shorter than jugal-prefrontal contact; and (4) anterior portion of elongate choana expanded slightly laterally, rather than straight-sided as in *Parioxys*, and rounded anteromedially, rather than angular as in *Cochleosaurus*.

A feature of *Chenoprosopus milleri* interpreted first by Williston (1918) as a premaxillary palatal tusk pair on the basis of FMNH UC 155 requires comment. The “tusks” are included in an early reconstruction of the palate (Romer, 1947), and their positions along the midline are approximated by dashed circles in the reconstruction provided by Langston (1953). This area is not exposed on *C. lewisi*. I have examined FMNH UC 155, which offers the largest known palate of the genus, and concur with Langston (1953:374) that these imperfectly preserved features are not tusks. Their anteromedial position coincides with a buttress found in the long-snouted loxommatid *Megalocephalus pachycephalus*; in that example, Beaumont (1977) suggested that the buttress served to reinforce the snout against sagittal shearing.

Most differences between *Chenoprosopus lewisi* and *C. milleri* relate to the size disparity between these taxa. The much smaller size of *C. lewisi* probably accounts for the presence of a pineal foramen (see discussion in following section), a proportionally longer postsplenial, and comparatively shorter snout and vomers. In *C. lewisi*, however, a short but indisputable nasal-maxilla contact separates the septomaxilla and lacrimal. Although an identical configuration was reconstructed for *C. milleri* by Langston (1953), his illustration of the principal specimen (UCMP 33439, his fig. 5) shows that the nasal-maxilla contact is absent or reduced to a point contact; examination of this and two other skulls of *C. milleri* confirms the condition depicted in his specimen drawing. I know of no primitive temnospondyls in which a nasal-maxilla contact is obliterated with growth. To the contrary, a nasal-maxilla contact is attained or elaborated with increased size in the eryopoids *Sclerocephalus* (Boy, 1988) and *Archegosaurus* (Meyer, 1858). Moreover, a nasal-maxilla contact is maintained in all specimens of both species of the long-snouted loxommatid *Megalocephalus* (Beaumont, 1977). I conclude that the greater nasal-maxilla contact of *C. lewisi* is a derived character for the species.

A primitive aspect of *C. lewisi* is an appreciable postorbital-supratemporal contact similar to that found in nearly all temnospondyls that possess an intertemporal. This contact is greatly reduced on the dorsal surface of the best preserved skull of *C. milleri* (UCMP 33439), which allows the squamosal to reach the posterolateral corner of the intertemporal. The left side of the smallest specimen of *C. milleri* (UCMP 34174) shows the primitive postorbital-supratemporal contact; this skull, however, was ground and etched to reveal sutures and does not necessarily reflect the condition of the dorsal surface. As illustrated by Steen (1938), the relationships between the postorbital and supratemporal, and therefore the squamosal and intertemporal, are variable in the much-flattened skulls of *Cochleosaurus bohemicus*, but it is not evident how or if this variation is related to size. Thus, I suggest that the intertemporal-squamosal contact of *Chenoprosopus milleri* be considered provisionally as a derived feature for the species.

The size and position of the vomerine tusks in *C. lewisi* resemble more closely those of *Cochleosaurus* than of *Chenoprosopus milleri*. In the latter taxon, the tusk is robust and situated anterior to the apex of the choana. In *C. lewisi*, the tusk is smaller than most of the maxillary teeth, the accompanying replacement pit also is reduced, and both are positioned near the anteromedial margin of the choana. Notably, the palatine tusk and pit are of the expected, larger size.

Table 1.—*Derived characters of (1) cochleosaurids and (2) edopoids reported recently in the literature (Godfrey and Holmes, in press; Sequeira and Milner, in press). See text for discussion.*

1. Cochleosaurid characters
1.1. Closure of parietal foramen in adults.
1.2. No lateral line sulci.
1.3. System of prominent, rounded ridges on skull roof that separate depressed areas of muted sculpture.
1.4. Squamosal lacks posterodorsal process; lateral edge of supratemporal exposed broadly along anterodorsal margin of otic notch.
1.5. Lateral ala of pterygoid contacts jugal, excludes ectopterygoid and maxilla from subtemporal fossa.
1.6. Extreme elongation of premaxillae and vomers produces elongate preorbital region and posterior position of both external and internal nares.
1.7. Large premaxillae with posterolaterally directed premaxilla-nasal sutures.
1.8. Elongate, triangular choanae wider anteriorly than posteriorly.
2. Edopoid characters
2.1. Enlarged premaxillaries with a long common median suture; small naris set well back along snout.
2.2. Jugal-prefrontal contact excludes lacrimal from orbit margin.

Relationships of Chenoprosopus

Since the time Langston (1953) considered the relationships of *Chenoprosopus*, our knowledge of potentially related forms from coal-bearing Upper Carboniferous rocks has improved thanks largely to the advent of acid-etching and latex-micro-casting preparation (Baird, 1955). Although these findings have yet to be presented in a detailed manner, several taxa described in earlier works are recognized now as incomplete remains of better represented species. Such junior synonyms include *Gaudrya latistoma* Fritsch [= *Cochleosaurus bohemicus* Fritsch: Sequeira and Milner, in press] and *Leptophractus dentatus* Moodie and *Mytaras macrognathus* Steen [= *Macrerpeton huxleyi* (Cope): Hook and Baird, 1986], among others. Over the same time period, discovery of new material in the Upper Carboniferous of Nova Scotia has provided a new species of *Cochleosaurus* (Rieppel, 1980; Godfrey and Holmes, in press) and has clarified some aspects of the primitive temnospondyl *Dendrerpeton* (Godfrey et al., 1987, and ongoing work). Additional specimens of *Dendrerpeton* have been described from Jarrow, Ireland, by Milner (1980b), who also noted a *Cochleosaurus*-like form in the same assemblage.

These advances and the discovery of the small *Chenoprosopus* specimen described here underscore Langston's close association of the "long-faced" forms *Chenoprosopus* and *Cochleosaurus*. But whereas Langston suggested the recognition of two separate families, the Chenoprosopidae and Cochleosauridae, additional data on both genera have revealed no major differences, and most subsequent workers have grouped these taxa together within the senior family, the Cochleosauridae. A second genus attributed to the Chenoprosopidae by Langston is *Macrerpeton* [*Mytaras*], a very odd temnospondyl known from less than five Linton specimens and two fragmentary examples from a recently discovered deposit at Five Points, Ohio (Hook and Baird, 1986, in press). Similarities with *Chenoprosopus* include an expansive snout and vomers; elongate choanae; and long, slender, slightly recurved maxillary teeth. Because a redescription of this poorly known material is underway, further commentary is premature.

The “long-faced” ramus of Langston’s bipartite edopoid phylogeny apposed several “short-faced” genera, of which only *Edops* has survived as a valid taxon. Unlike the cochleosaurids and *Dendrerpeton*, no additional data of significance have come forth recently on *Edops*, and it continues to be known mainly from an extremely large, incomplete skull from the Lower Permian of Texas (Romer and Witter, 1942). Unfortunately, this troublesome form is the basis for the superfamily Edopoidea, which consists at present of the Edopidae and Cochleosauridae.

Recent studies by Godfrey and Holmes (in press), Milner and Sequeira (in press), and Sequeira and Milner (in press) have included cladistic analyses of the Cochleosauridae and the Edopoidea. Although these efforts have corrected errors of previous contributions, I believe that critical questions of character polarity and significance remain. Table 1 presents the characters put forth by these authors for cochleosaurids and edopoids; in some cases, I have modified slightly the original statements in order to simplify expression.

Character 1.1, closure of the parietal foramen in adults, is problematic because a well-ossified specimen of the Linton cochleosaurid (AMNH 6954) with an estimated minimum skull length of 130 mm has a pineal foramen. The opening also is present in *Chenoprosopus lewisi*, which falls within the size range of the skulls of *Cochleosaurus florensis* (skull lengths from 84 to 123 mm), all of which have no foramen. The smallest skull of *Chenoprosopus milleri* (length of 189 mm) lacks the opening. Pending a more complete documentation of the parietal foramen in the single-population growth series of *Cochleosaurus bohemicus*, I regard this character as provisional at the family level.

The lack of lateral line sulci (Godfrey and Holmes, in press), character 1.2, is of practical use in identifying fragmentary cochleosaurid remains but can be assigned little phylogenetic significance. Likewise, the system of ridges and depressions on the skull roof and associated variations in dermal sculpture (character 1.3) occurs in a great number of other forms, including panderichthyid fishes (Schultze and Arsenault, 1985), loxommatid amphibians (Beaumont, 1977), and many dissorophoid and eryopoid-grade (especially zatrachydids) temnospondyls, and appears to be of little value in a discussion of relationships.

Godfrey and Holmes (in press) cite the lack of a posterodorsal process on the squamosal and the resulting contribution of the supratemporal to the dorsal rim of the otic notch (character 1.4) as a derived character for cochleosaurids. As noted correctly by Sequeira and Milner (in press), however, the supratemporal is the dominant element on the dorsal rim of the otic notch in many temnospondyls, and the squamosal-supratemporal configuration is only of consequence if a close relationship between cochleosaurids and *Edops* is accepted.

In cochleosaurids, a jugal-pterygoid suture precludes the maxilla and ectopterygoid from the subtemporal fossa and prevents a maxilla-quadratojugal contact (character 1.5). This suture is more extensive and complex than that found in some saurerpetontid trimerorhachoids (*Acroplous*: Foreman, 1990; possibly *Saurerpeton* and *Erpetosaurus*). Although the maxilla has a short contact with the quadratojugal in *Edops* (Romer and Witter, 1942), the participation of either the pterygoid or ectopterygoid in the anterolateral closure of the subtemporal fossa cannot be assessed from the available material.

Detailed aspects of the elongate cochleosaurid snout are addressed by characters 1.6, 1.7, and 1.8. Extreme elongation of the premaxillae and vomers (character 1.6 in part) occurs also in archegosaurids and some trematosauroids, but these

taxa generally lack the more posteriorly positioned narial openings of cochleosaurids. Character 1.7, large premaxillae with posterolaterally directed premaxilla-nasal sutures, was treated with reservation by both Godfrey and Holmes (in press) and Sequeira and Milner (in press) because a similar condition exists in *Edops*.

An attribute of cochleosaurids that Godfrey and Holmes (in press) mention but which does not appear in their character list is the pterygoid-cultriform configuration. Though difficult to determine in most specimens, the pterygoids appear to contact the cultriform process but fail to join each other anteriorly. A nearly identical arrangement was described by Moustafa (1955) in the supposed eryopoid *Parioxys* from the Lower Permian of north-central Texas (Carroll, 1964). A full reinvestigation of this genus, which also has elongate choanae, may have a significant impact on existing hypotheses of edopoid-eryopoid relationships.

The edopoid characters of Table 1 are those that are said to unite the cochleosaurids and edopids in a primitive clade (Sequeira and Milner, in press). Character 2.1, premaxillary elongation associated with small, inset external nares, encompasses much of characters 1.6 and 1.7. A prefrontal-jugal exclusion of the lacrimal from the orbit (character 2.2) is found also in eryopoids (Milner, 1978) and, therefore, is not a unique shared derived character of edopoids.

To summarize, I regard the following characters as cochleosaurid synapomorphies: (1) elaborate jugal-ptyergoid suture excludes maxilla and ectopterygoid from subtemporal fossa, (2) vomers elongated anterior to choanae, and (3) choanae elongate and wide anteriorly. The union of *Edops* and cochleosaurids within the Edopoidea appears to be supported strongly by only one synapomorphy: small inset external naris bordered by elongate premaxilla.

Most discussions of *Chenoprosopus* have noted similarities with *Archegosaurus*, a long-snouted eryopoid from the Lower Permian of Europe (Mehl, 1913; Romer, 1947; Langston, 1953). A close relationship between these two genera has been expressed recently in cladistic terms by Boy (1990), who also emphasized the tenuous nature of a close association between *Edops* and *Chenoprosopus*. If the hypothesis put forth by Boy is correct, the cochleosaurids represent the base of a lineage that culminated eventually in stereospondyls, and neither the Edopoidea nor the Eryopoidea are monophyletic.

Of the synapomorphies just noted, *Archegosaurus* has only the second cochleosaurid character, vomers elongated anterior to the choanae. It does, however, have a nasal-maxilla contact that is similar to that of *Chenoprosopus lewisi* and elongate, triangular prefrontals comparable to those of cochleosaurids (apomorphic characters 25 and 26 of Boy, 1990). Additional features of undetermined polarity shared by *Archegosaurus* and cochleosaurids include antorbital length greater than midorbital width, elongate premaxilla, modest tabular horns, and a simple iliac blade with only a rudimentary posterior process.

Sequeira and Milner (in press) rejected Boy's hypothesis largely on the basis of characters used by Milner (1989) in a cladistic synopsis of European eryopoid-grade temnospondyls. Among the derived characters reported by Milner for "higher temnospondyls" (taxa other than the dendrerpetontids, edopoids, and trimororhachoids; loxommatids and colosteoids are not considered as temnospondyls) that appear to refute most convincingly a close relationship between *Chenoprosopus* and *Archegosaurus* are: (1) premaxilla with narrow marginal ramus and distinct alary process bordering large external naris, and (2) reduced basioccipital and enlarged exoccipitals resulting in bilobed occipital condyle. The premaxillary character requires comment because at least two types of alary processes may be

recognized. In one variety, the process terminates on the medial margin of the external naris, and the nasal-premaxilla suture remains fairly straight; as seen in *Archegosaurus*, this configuration can be derived directly from a cochleosaurid with small external nares simply by enlarging the narial opening. A second and more common sort of alary process, typified by *Eryops*, is set off distinctly from the external naris and affects a posteriorly directed V in the nasal-premaxilla suture. Because this “free” alary process occurs also in *Capetus*, a problematic Upper Carboniferous temnospondyl that lacks the prefrontal-jugal contact of both edopoids and eryopoids (Sequeira and Milner, in press), it may represent a primitive condition.

The second character considered as derived by Milner (1989) and Sequeira and Milner (in press) for higher temnospondyls also invites debate. The transition from a single occipital condyle to a bilobed or double configuration is known to have been achieved independently in other lineages, such as the trimerorhachid-saurerpetontid-brachyopid clade (Coldiron, 1978). Consequently, it could be argued that the exoccipital-dominated arrangement of archegosaurids developed from a cochleosaurid stock quite separate from a zatrachydid-eryopid-dissorophoid group. Other characters reported by Milner (1989) or by Sequeira and Milner (in press) as derived for archegosaurids within a higher temnospondyl clade could be obtained independently by slight modification of a *Chenoprosopus*-like cochleosaurid, including an extremely high skull length-width ratio, no intertemporal, paired anterior palatal vacuities, loss of the pterygoid flange, vomer and palatine contributions to the interpterygoid vacuities, and accessory palatal dentition.

Inasmuch as *Chenoprosopus* and *Archegosaurus* are roughly contemporaneous Lower Permian taxa of very similar ecomorphotypic plans but without geographic overlap, it is tempting to seek a common ancestral form in the Upper Carboniferous. *Cochleosaurus* certainly is not a candidate despite its cosmopolitan record in the late Westphalian, and the poorly known *Macrerpeton* similarly is too specialized. As noted by Milner and Sequeira (in press), there are cochleosaurid fragments from the Westphalian B of Joggins (Carroll, 1967:text-fig. 7A as *Dendrerpeton*), and somewhat older and more complete material from Jarrow (Milner, 1980b). The origin of cochleosaurids and a resolution of their relationships must be sought in yet-to-be-collected pre-Westphalian deposits.

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THE PELYCOSAURIAN (AMNIOTA: SYNAPSIDA) ASSEMBLAGE
FROM THE LATE PENNSYLVANIAN SANGRE DE CRISTO
FORMATION OF CENTRAL COLORADOSTUART S. SUMIDA¹

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ABSTRACT

A diverse assemblage of pelycosaurian-grade synapsids is described on the basis of fragmentary remains from a highly fossiliferous quarry of Late Pennsylvanian, probably Missourian, age in the Sangre de Cristo Formation of central Colorado. The fragmentary nature of the materials precludes in most instances assignment below family or subfamily, or the erection of new taxa. Identifications include at least one member each of the families Ophiacodontidae, Sphenacodontidae, and Haptodontidae, and two members of the Edaphosauridae, one referable to *Ianthasaurus* and the other to a new but unnamed genus and species. Only the extremely productive Garnett quarry of eastern Kansas and El Cobre Canyon in northern New Mexico have yielded as many Pennsylvanian-aged pelycosaurian taxa with certainty.

INTRODUCTION

Localities of Pennsylvanian age that yield remains of terrestrial tetrapods are extremely rare, and those that produce pelycosaurian-grade synapsids are even fewer in number. Of the well-known North American localities (Table 1), Vaughn (1969, 1972) described one in central Colorado that includes as many or more species of pelycosaurs than any other in the world. The quarry, designated as the "Badger Creek locality" by Milner and Panchen (1973) in their review of Late Paleozoic tetrapod faunas and localities, is in the Sangre de Cristo Formation near the town of Howard in the Arkansas River valley of Fremont County, Colorado. Vaughn (1972:2) described the productive level of the quarry as a two- to three-foot-thick black shale that is a "lens-shaped deposit that probably represents a pond, perhaps an oxbow within the general system of stream channels indicated in this part of the formation." The black shale unit was designated by Brill (1952) as part of "Interval 300," lying approximately 442 m above the base of the 2933 m-thick Sangre de Cristo Formation. It lies in NW $\frac{1}{4}$ NE $\frac{1}{4}$ SW $\frac{1}{4}$ Sec. 22, T. 49 N, R. 10 E. Vaughn estimated that the deposit is of Late Pennsylvanian age, most likely Missourian, primarily on the basis of the vertebrate assemblage; however, he also considered geological evidence based on the work of Mallory (1958, 1960).

Although specimens from the Badger Creek locality are rarely complete, they show little or no sign of surface wear. This has facilitated identification of a highly diverse assemblage that, in addition to pelycosaurs, includes elasmobranch and palaeoniscoid fishes, labyrinthodont, aistopod, and microsaurian amphibians, the enigmatic diadectomorphs *Desmatodon* and *Limnoscelis*, and protorothyridid reptiles (Vaughn, 1969, 1972; Berman and Sumida, 1990).

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Table 1.—Numbers of pelycosaurian taxa from Pennsylvanian localities in North America. Localities are listed in approximate order from east to west. * Pittsburgh is actually two (or more) deposits.

Locality	Number of pelycosaur taxa	Reference
Florence, Nova Scotia	5	Reisz, 1972
Joggins, Nova Scotia	1(?)	Carroll, 1964
Pittsburgh, Pennsylvania*	2	Romer, 1952, 1961
Elm Grove, West Virginia	1	Berman, 1979
Linton, Ohio	1	Hook and Baird, 1986
Danville, Illinois	1	Cope, 1875
Jasper County, Illinois	1	De Mar, 1970
Robinson, Kansas	1	Chorn and Schultze, 1990
Garnett, Kansas	5	Reisz, 1990
Hamilton, Kansas	1	Schultze and Chorn, 1988
Badger Creek, Colorado	5	This paper
El Cobre Canyon, New Mexico	7	Berman, in press

Vaughn (1972) recognized the presence of four pelycosaurian taxa among the Badger Creek materials. Additional preparation, however, has revealed at least five different pelycosaurs. Only the localities of Garnett, Kansas, and possibly Florence, Nova Scotia, have yielded as many different kinds of Pennsylvanian pelycosaurs. The Badger Creek remains include at least one member each of the family Ophiacodontidae and the subfamilies Sphenacodontinae and Haptodontinae, and two members of the Edaphosauridae, one referable to *Ianthasaurus* and the other to a new but unnamed genus and species.

All of the specimens described in this study were collected by Peter Vaughn and cataloged into the University of California, Los Angeles, vertebrate paleontology collections (UCLA VP). In 1987, this collection, as well as others from the Permo-Pennsylvanian at that institution, were transferred permanently to the Carnegie Museum of Natural History, Pittsburgh (CM).

SYSTEMATIC DESCRIPTIONS

Recent analyses of the phylogenetic relationships of primitive amniotes (Gauthier et al., 1988; Berman et al., 1992) have proposed the Synapsida as amniotes separate from a more narrowly defined Reptilia. No subsequent proposal of nomenclature regarding the class designation of pelycosaurs, traditionally referred to as “mammal-like reptiles,” has been forthcoming. For that reason, class designations have been omitted in the following systematic descriptions.

Subclass Synapsida
Order Pelycosauria
Family Ophiacodontidae

Materials.—CM 31389, greater part of left humerus (Fig. 1A, B); CM 47693 (formerly UCLA VP 1695), partial neural arch; CM 47694 and 47695 (formerly UCLA VP 1696 and 1697), partial right and left ilia, respectively; CM 47696, part and counterpart blocks that include associated elements of most of left hindlimb and foot, right femur, and gastralia; CM 47705, nearly complete right pelvic girdle (Fig. 1C).

Description.—Though no cranial materials attributable to Ophiacodontidae are preserved, several postcranial elements exhibit features characteristic of the fam-

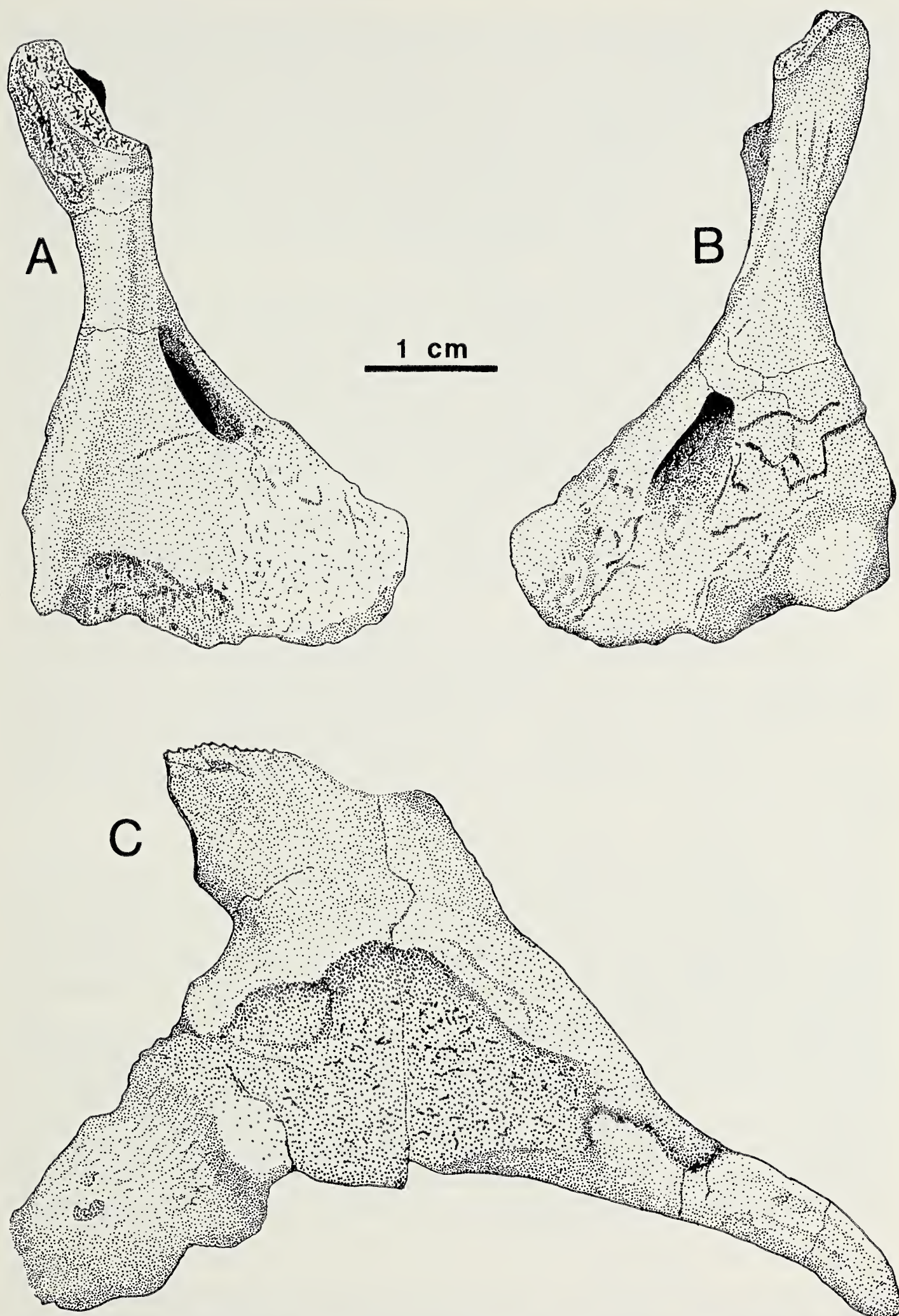


Fig. 1.—Ophiacodontid. A, B, distal dorsal and distal ventral views of left humerus CM 31389; C, lateral view of right pelvis CM 47705.

ily. Vaughn (1969) identified a partial neural arch, retaining only the left posterior zygaphophysis and base of the spine (CM 47693), and partial right and left ilia (CM 47694 and 47695 respectively) as ophiacodontid and appropriate to one another in size. Vaughn (1969) considered the neural arch as undoubtedly ophiacodontid, noting the laterally compressed blade-like structure of the spine and the absence of any lateral excavation of the neural arch. His assignment of the ilia was less certain, noting only their close similarity to those of Lower Permian *Ophiacodon* species figured by Romer and Price (1940) and the absence of features of other well-known groups. The ilia are of the same size and could very likely belong to the same individual.

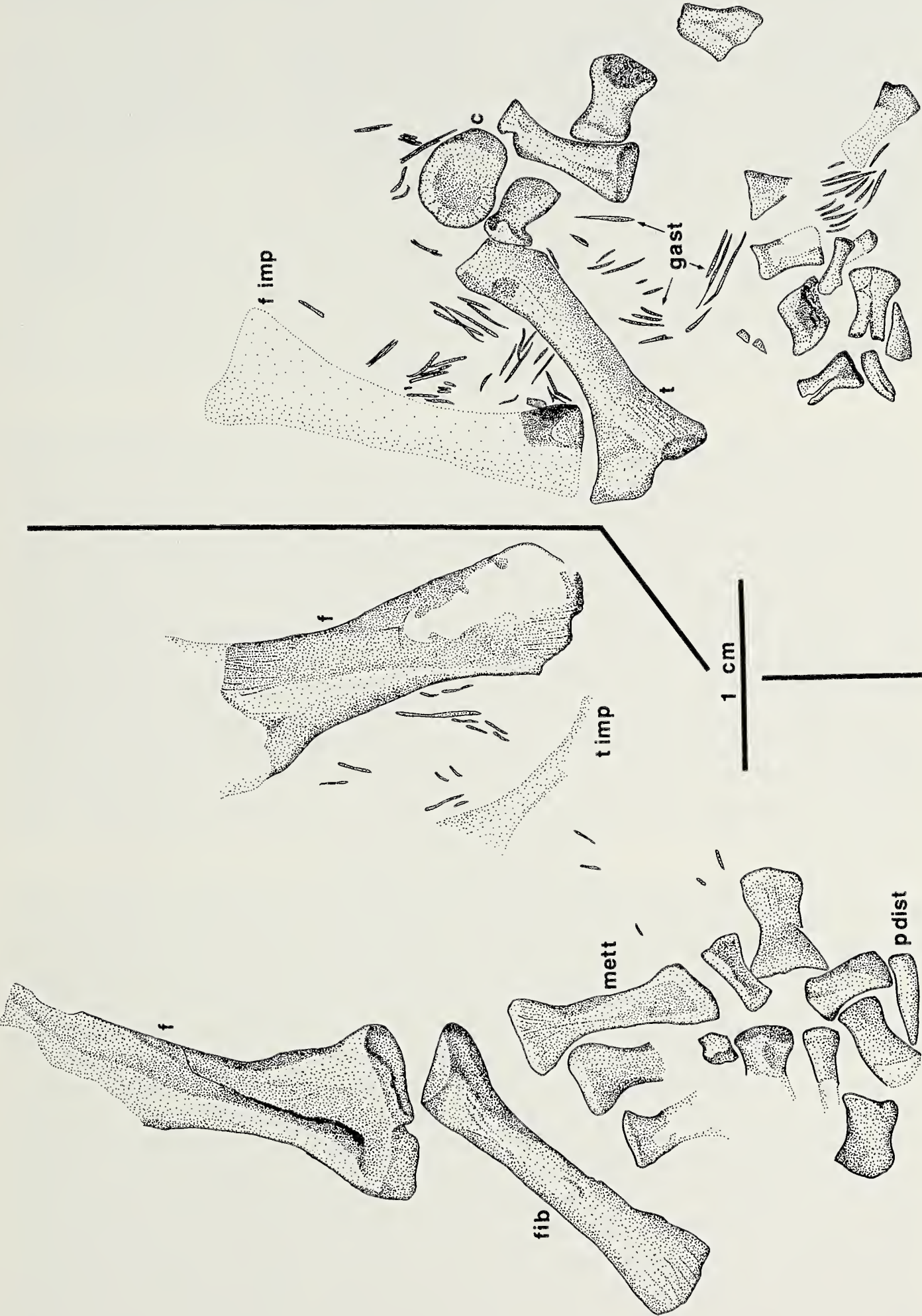
Several other postcranial elements now recognizable from the Badger Creek locality help to confirm the presence of an ophiacodontid. This is particularly true of a nearly complete right pelvis (CM 47705, Fig. 1C). It is much smaller than that represented by the ilia CM 47694 and 47695, yet its sutures are not distinct. Although the distal tip of the iliac blade is missing, there is no doubt that the ilium tapered as it curved strongly posteriorly in typical ophiacodontid fashion. As in other pelycosaurs, within the rather simple, horizontally oval acetabular depression is a roughly triangular unfinished articular surface. A thin, poorly developed ridge defines the apex of the articular surface, which has the outline of a low, rounded, posteriorly directed wave crest. The ischium is a smoothly finished quadrangular plate, whereas the pubis is extremely slender and lightly built.

A humerus (CM 31389, Fig. 1A, B; see also Sumida, 1989a, fig. 15D) exhibits an extremely well-developed and elongate entepicondyle that is characteristic of the family. The distal terminus of the entepicondyle is rugose on both dorsal and ventral surfaces, presumably for the attachment of extensor and flexor musculature of the antebrachium, respectively. The ectepicondyle and tip of the supinator process are chipped away, but a groove that begins well up the slender shaft clearly separated them as in *Ophiacodon* (Reisz, 1986). Most of the proximal articular surface has been lost.

Part and counterpart blocks (CM 47696, Fig. 2) preserve most of an ophiacodontid left hindlimb and foot, greater part of the right femur, and numerous scattered gastralia. As is common in ophiacodonts, the articular surfaces of the limb bones are largely unossified. Both femora are visible in dorsal aspect only, and little description may be added beyond what is visible in Fig. 2. The tibia is approximately 65% of the length of the femur. The shaft of the tibia appears to be dorsoventrally compressed.

Elements of the hind foot are scattered and incomplete but sufficient to make some general comments. What appears to be the calcaneum is subcircular in outline, with the margins being thickened slightly over the central area. A notch for a perforating artery is not obvious in the specimen. What may be the neck of the astragalus is preserved adjacent to the calcaneum. The metatarsal elements are much longer than the phalanges. Although the jumbled nature of phalangeal elements prevents a detailed description, the presence of a claw-like distal phalanx

Fig. 2.—Ophiacodontid CM 47696, part and counterpart blocks showing associated elements of most of left hindlimb and foot, right femur, and scattered gastralia. Abbreviations: c, calcaneum; f, femur; fib, fibula; f imp, impression of femur; gast, gastralia; mett, metatarsal elements; p dist, distal phalanx; t, tibia; t imp, impression of tibia.



is notable. The phalanges are not broad and flattened as in some ophiacodonts such as *Ophiacodon* sp. (Romer and Price, 1940), indicating that the Badger Creek form may represent a primitive member of the family.

Gastralia are scattered among the hindlimb elements of CM 47696. None demonstrate the V-shaped bar appearance of the midline gastralia described in *Ophiacodon* (Romer, 1956). They are all thin, simple, rod-shaped elements similar to the more distal, lateral components of the ventral dermal armor described by Williston and Case (1913) in *Ophiacodon*.

Vaughn (1972) noted briefly the occurrence of an isolated basiparasphenoid (CM 47653, formerly UCLA VP 1740) among the Badger Creek materials that he believed to be ophiacodontid. This element actually belongs to a partial, disarticulated skeleton that was designated as the holotype of a new species of *Limnoscelis*, *L. dynatis* (Berman and Sumida, 1990).

Family Sphenacodontidae Subfamily Sphenacodontinae

Materials.—CM 34447, sacral vertebra (Fig. 3D); CM 34448, marginal tooth; CM 47702 (formerly UCLA VP 1704), partial left premaxilla (Fig. 3A); CM 47704 (formerly UCLA VP 1741), dorsal vertebra (Fig. 3B, C).

Description.—What Vaughn (1969) described as a fragmentary right maxilla of a sphenacodontine is reinterpreted here as a partial left premaxilla (CM 47702, Fig. 3A). The reinterpretation is based mainly on the presence of a large, well-preserved maxillary process that was laterally overlapped by the maxilla, and a large, flat symphyseal surface that contacted its mate on the midline. In general, the premaxilla compares closely to that in *Sphenacodon* (Eberth, 1985); however, it appears to possess only two robust teeth rather than three, and the second tooth (7 mm long) is considerably shorter than the first (11 mm long). As described by Vaughn (1969), the teeth are flattened slightly mediolaterally, broadly based, and distally pointed. The maxillary process angles posterodorsally, as is characteristic of sphenacodontines. The body of the premaxilla is robustly constructed, more so than those assigned to *Haptodus* (see below), as has been discussed by Reisz et al. (1992).

A nearly 15 mm-long isolated tooth (CM 34448), of somewhat different character, is nonetheless clearly sphenacodontid in nature. It is recurved and mediolaterally compressed. Distinct, low, very narrow cutting edges extend nearly the entire fore and aft lengths of the tooth, passing through the tip of the crown. The cutting edges are accentuated by a very shallow, parallel depression on what is probably the lingual surface of the tooth. This general morphology is in contrast to the somewhat more bulbous teeth assigned here to *Haptodus* (see below).

Vaughn (1972) noted the presence of a small sphenacodontid dorsal vertebra, CM 47704 (Fig. 3B, C), consisting of a centrum and neural arch with only the base of the neural spine preserved. A sphenacodontid sacral vertebra, CM 34447, of similar size and proportion is also present among the Badger Creek materials (Fig. 3D). As preserved, the vertebrae do not exhibit any features that would positively identify them as belonging to either a sphenacodontine or haptodontine. Assignment to the Sphenacodontidae rather than the Haptodontidae is based on the relatively much deeper lateral excavations in the neural arch just above the transverse processes and the very deep longitudinal excavations of the lateral surfaces of the centrum that result in the greatly flared rims. Reisz and Berman (1986) described similar but much shallower excavations in the primitive eda-

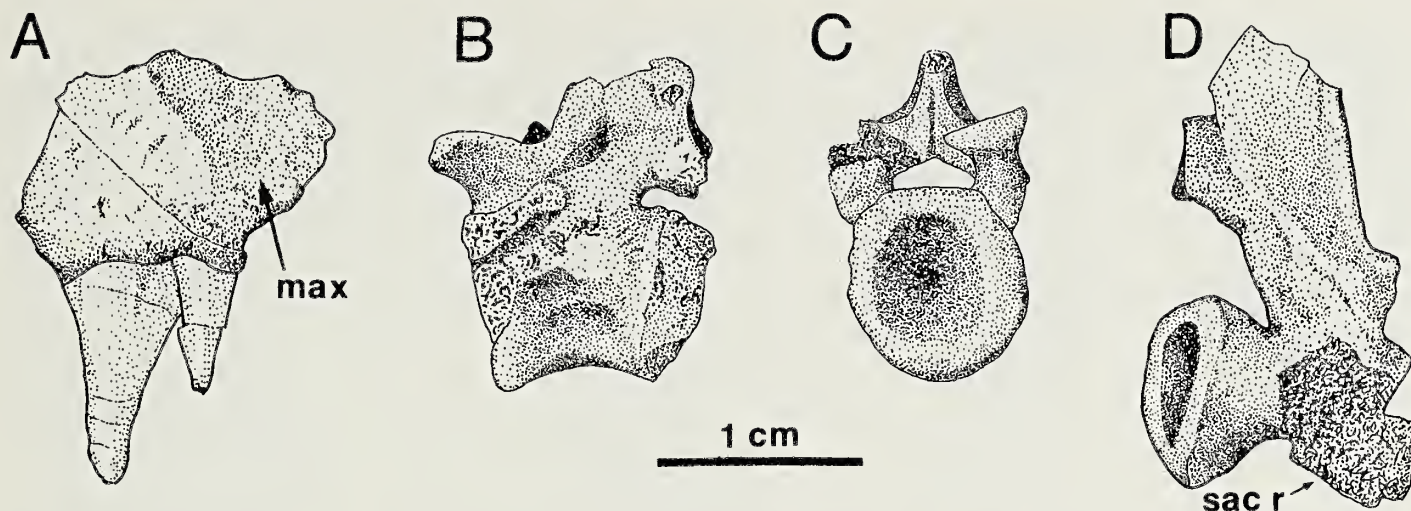


Fig. 3.—Sphenacodontid. A, lateral view of partial left premaxilla CM 47702; B, C, left lateral and anterior views of incomplete dorsal vertebra CM 47704; D, right posterolateral view of partial sacral vertebra CM 34447. Abbreviations: max, maxillary suture; sac r, articulation for sacral rib.

phosaur *Ianthasaurus*. Further, the configurations of the neural arch and associated spine are unlike those of the edaphosaurs found at Badger Creek. Brinkman and Eberth (1983) have pointed out that the varanopseid *Varanops* also possesses depressions of the neural arch, but their position is relatively more posterior. The midventral region of the centrum of CM 47704 is not sharply keeled, and the transverse processes, though broken, appear to be very small, indicating a position in the posterior region of the presacral column. Though only the base of the neural spine is present, its outline in horizontal section at the break is suggestive of a blade-like structure. In the sacral vertebra CM 34447 (Fig. 3D) the rib has been broken away and the cross-sectional area of the break is indicative of the first or second sacral vertebra. It also possesses the characteristic excavation of the neural arch and retains a blade-like neural spine. The costal articulations are stoutly buttressed.

Family Haptodontidae Subfamily Haptodontinae

Materials.—CM 34443, partial right pterygoid (Fig. 4D); CM 34444, portion of right scapula (Fig. 4H); CM 34445, partial right femur (Fig. 4I); CM 34446, partial right dentary (Fig. 4E–G); CM 47701 (formerly UCLA VP 1749), left premaxilla (Fig. 4A, B); CM 47703, left premaxilla (Fig. 4C).

Description.—A right dentary, CM 34446 (Fig. 4E–G), is the most distinctly haptodontid element preserved at Badger Creek. The pattern of surface sculpture is very similar to that of *Haptodus garnettensis* (Laurin, in press), consisting of a series of fine, shallow, irregularly placed, interconnected pits and grooves. The teeth are sphenacodontid in nature, but show little of the differentiation characteristic of *Sphenacodon*, *Dimetrodon*, and other advanced sphenacodontids. In contrast to most sphenacodontids, the depth of the preserved anterior portion of the dentary remains uniform and is relatively much deeper throughout its length. In sphenacodontids there is a distinct narrowing of the dentary just before the symphyseal region, where it deepens in a strong dorsalward expansion. The expansion, with its greatly developed teeth, is accommodated by a corresponding dorsalward, step-like concavity of the ventral margin of the maxilla and the premaxilla, where there is a reduction or gap in the marginal dentition.

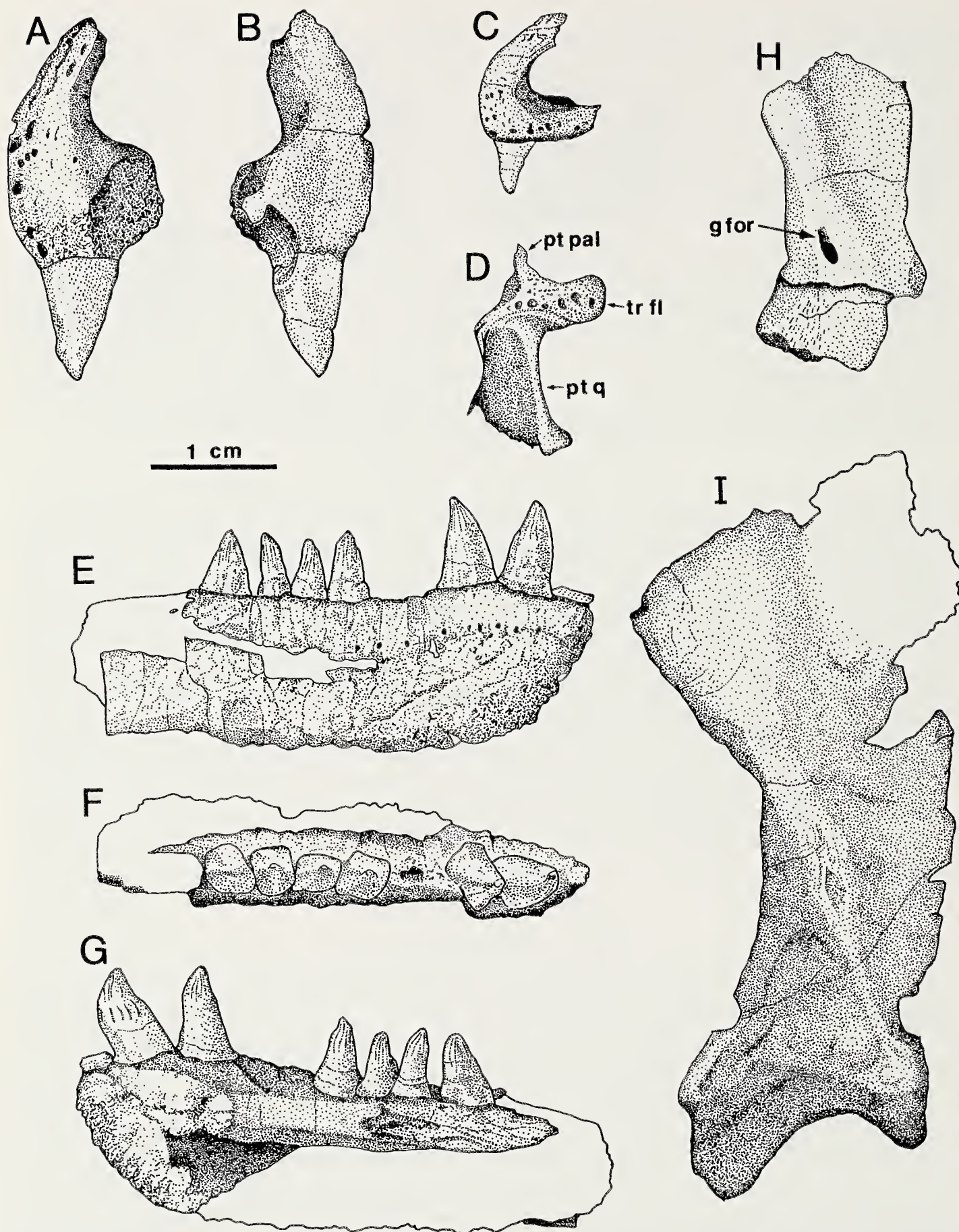


Fig. 4.—Haptodontine. A, B, lateral and medial views of larger left premaxilla CM 47701; C, lateral view of left premaxilla CM 47703; D, ventral view of partial right pterygoid CM 34443; E–G, lateral, dorsal, and medial views of partial right dentary CM 34446; H, lateral view of partial right scapular blade CM 34444; I, ventral view of right femur CM 34445. Abbreviations: g for, glenoid foramen; pt pal, palatal ramus of pterygoid; pt q, quadrate ramus of pterygoid; tr fl, transverse flange of pterygoid.

The symphyseal suture is rugose and approximately triangular in outline. The absence of a splenial reveals a moderately developed alveolar shelf along the dorsal margin of the medial surface of the dentary. Six teeth are preserved in the dentary, with a gap for another between the second and fourth. The teeth are somewhat bulbous and more stoutly conical than in other specimens of *Haptodus*. The third tooth appears to be permanently lost, inasmuch as the alveolus is completely filled with bone. Unlike spenacodontids, but as occurs in some *Haptodus* specimens, the first two teeth are subequal in size and not greatly enlarged over those of the rest of the series. The posterior four teeth of the series are subequal in size. They are similar to those of *Haptodus* in being essentially simple, subconical structures. The bases, approximately the lower two-thirds of the teeth, are subcircular to quadrangular in horizontal section, whereas the crowns are circular with a slight posterolingual curvature. Shallow, minute grooves on the crown converge on the sharply pointed tip. In clear contrast to the marginal teeth of spenacodontids, they are not compressed labiolingually and lack fore and aft cutting ridges. As with the premaxillary tooth, they are only slightly recurved. Although the two anteriormost teeth are larger than the rest, they do not show the extreme hypertrophy common to more advanced spenacodontids.

The two left premaxillae, CM 47701 and 47703 (Fig. 4A–C), are of quite different sizes, but both are assigned to the Haptodontidae on the basis of the strong similarity of their surface sculpturing and tooth morphology to that of the partial dentary described above. Both premaxillae possess a large, anteriormost tooth, but sockets for two smaller, posterior teeth are present in the smaller, more complete specimen. The large, anteriormost tooth projects normal to the ventral plane of the body of the premaxilla, and its tip is only slightly recurved as in *Haptodus*. The distal portion of the dorsal process in the larger specimen is lost, but is clearly stouter than that of the smaller specimen.

A partial right pterygoid, CM 34443 (Fig. 4D), includes the transverse flange, quadrate ramus, and proximal portion of the palatine ramus. Although typically spenacodontian in construction, it is too small to be associated with the robust spenacodontid premaxilla described above. As in *Haptodus* specimens described by Currie (1979), the transverse process bears approximately six teeth. However, in contrast to those specimens described by Currie (1979), the transverse flange is more stoutly built and slightly expanded distally, giving it a nearly triangular outline. A very fine ridge parallels its posterior margin. The ventral margin of the quadrate ramus is thickened, and the medial surface dorsal to it is slightly concave. There is no distinct facet for the basiptyergoid process of the braincase. Little can be said about the palatine ramus other than that it was necessarily a narrow element.

A partial right scapula, CM 34444 (Fig. 4H), is characteristic of spenacodontid and haptodontid pelycosaurs in being anteroposteriorly narrow. The supraglenoid buttress is well-developed and angles back to form the posterior border of the element. The supraglenoid foramen is placed directly on the crest of the buttress, a position also seen in *Haptodus baylei* (Currie, 1979:fig. 9) and considered possibly more primitive than the more anterior position in spenacodontids.

Of the pelycosaurian material described here, the femur CM 34445 (Fig. 4I) is probably the most poorly preserved, and its taxonomic assignment is made with the least amount of confidence. Despite the extreme dorsoventral crushing, it still exhibits general spenacodontian features. It is similar in size and general morphology to *Haptodus garnettensis* (Currie, 1977), although the development of

processes and ridges appears to be somewhat greater. The ventral adductor ridge is well-developed and expanded proximally into what Romer and Price (1940) termed the fourth trochanter for attachment of the caudifemoralis musculature (Sumida, 1989a). The midlength of the adductor ridge is marked by an oval pit of unknown function. The extent of the intertrochanteric fossa cannot be determined due to crushing. The intercondylar fossa of the distal, dorsal surface does not extend far up the femoral shaft.

Family Edaphosauridae
Ianthasaurus sp.

Materials. —CM 34449, partial right maxilla (Fig. 5A); CM 34500 and 34576, partial neural spines (Fig. 5B, C); CM 34577, dorsal vertebra with only base of neural spine (Fig. 5D); CM 34578, dorsal portion of right scapular blade (Fig. 5E); CM 34579, left femur (Fig. 5F, G); CM 34580, left astragalus (Fig. 5H, I); CM 34581, partial right femur; CM 47700, numerous, isolated centra and neural spines.

Description. —On the basis of neural spine morphology, two different edaphosaurids are identified from the Badger Creek locality. One form is recognized on the basis of a single unique neural spine (described below), whereas numerous isolated elements, most importantly vertebral neural spines with typical edaphosaurid lateral tubercles, are assigned to *Ianthasaurus*. There are only two well-known Pennsylvanian-aged edaphosaurs: *Edaphosaurus colohistion* from the Pittsburgh Formation, Monongahela Group of West Virginia (Berman, 1979), which probably reached a length of over 2 m, and *Ianthasaurus hardestii* (Reisz and Berman, 1986; Modesto and Reisz, 1990b), the most primitive member of the family from the Garnett Quarry of eastern Kansas, which probably reached a maximum length of 1 m.

With the realization that *Ianthasaurus* is significantly different from *Edaphosaurus*, Modesto and Reisz (1990a) questioned the assignment of other small, Late Pennsylvanian edaphosaurids to *Edaphosaurus* on the basis of fragmentary vertebral evidence. They argued that *E. raymondi* Case (1908), based on a small neural spine fragment, should be considered a nomen vanum and that *E. mirabilis* Fritsch (1895), based on a very small vertebra from Kounova, Czechoslovakia, may be closely related to *I. hardestii*. Further, Modesto and Reisz (1990a) recommended that the edaphosaurid material described here from the Late Pennsylvanian Sangre de Cristo Formation of Colorado and considered by Vaughn (1969) to show close affinities to *E. raymondi* be assigned to the Edaphosauridae as incertae sedis. However, all of the Badger Creek edaphosaurid remains, excluding only the single unique neural spine referred to above (and described below), are comparable in size and morphology to *Ianthasaurus hardestii* and can be assigned reasonably to that genus. The only noticeable difference between them is a higher degree of ossification and development of processes of the appendicular elements in the Badger Creek form.

Though none of the neural spines (Fig. 5B–D) are complete, some are complete enough to allow a composite description. The longest spine fragment is 4.8 cm long. As its diameter remains little changed throughout its length, the neural spine was undoubtedly well over 5 cm long. The spines are subcircular in cross section except for a very short proximal distance, where they are laterally compressed and have a slightly greater anteroposterior dimension. This proximal portion of

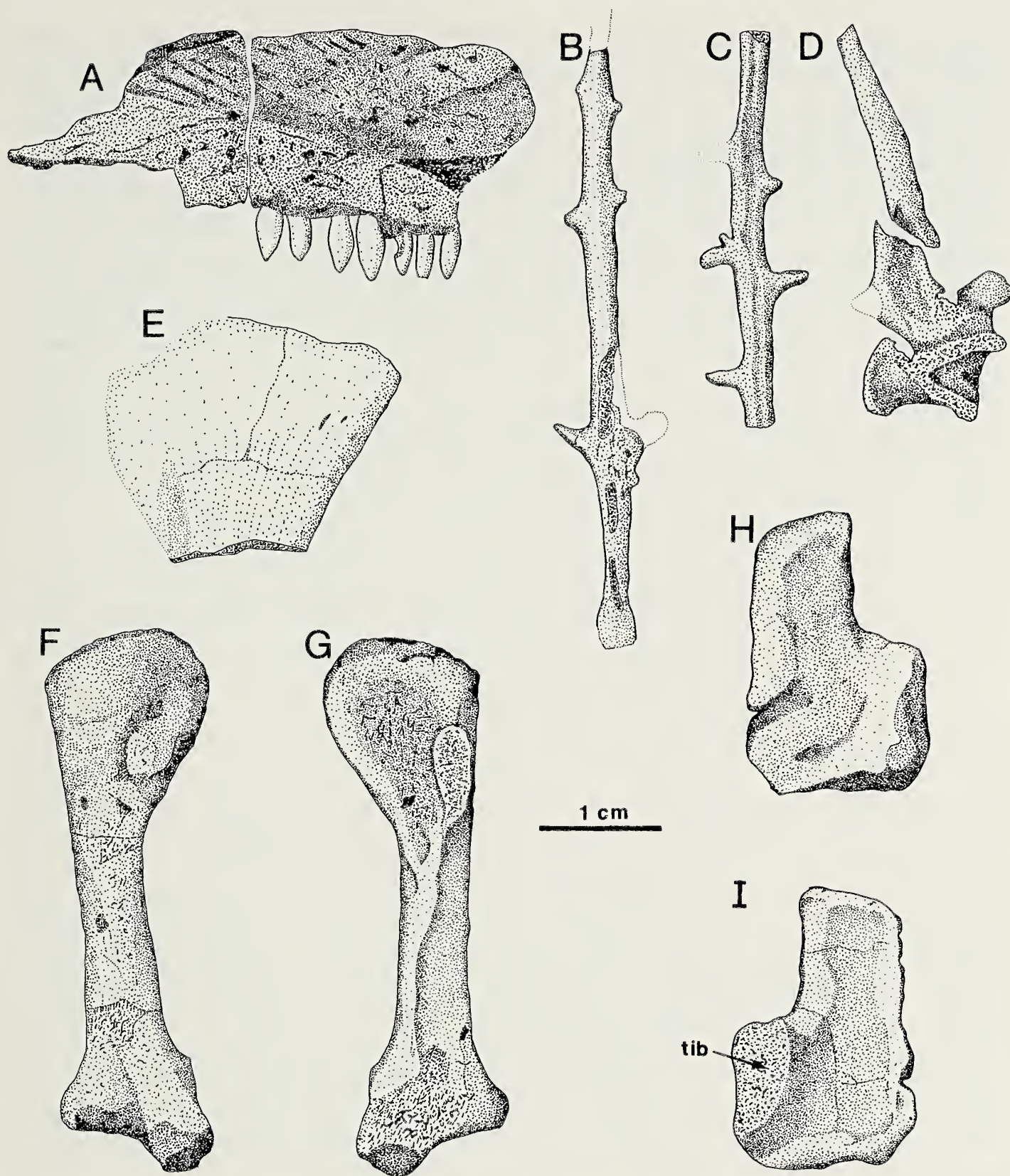


Fig. 5.—*Ianthasaurus* sp. A, lateral view of partial right maxilla CM 34449; B, C, anterior(?) views of isolated neural spines CM 34500 and CM 34576, respectively, that demonstrate variability in morphology of lateral tubercles; D, right lateral view of posterior dorsal vertebra CM 34577; E, lateral view of dorsal portion of right scapula CM 34578; F–G, dorsal and ventral views of left femur CM 34579; H, I, dorsal and ventral views of left astragalus CM 34580. Abbreviation: tib, tibial articulation.

the spine is not as blade-like as in the sphenacodontine vertebra described above. A narrow furrow extends along the anterior and posterior surfaces of the spine.

The presence of lateral tubercles of the neural spines is characteristic of edaphosaurids, the only exception being the Lower Permian *Lupeosaurus* (Sumida,

1989b). They are present on all but a few of the elongate neural spines of the Badger Creek specimens here assigned to *Ianthasaurus*. The absence of the lateral tubercles in some cases, including the bilaterally symmetrical basal pair (Fig. 5D), is a condition identical to that in the posteriormost region of the column in *Ianthasaurus* (Reisz and Berman, 1986). The lateral tubercles of the Badger Creek *Ianthasaurus* are quite knobby in appearance and are occasionally expressed as bifid, branched structures (Fig. 5C). As in other edaphosaurs, the basal tubercles differ from more distal ones in being much more strongly developed and occurring always as bilaterally symmetrical pairs. The neural arches display a slight excavation. This condition differs from that in the sphenacodontine described above in that the excavation continues well up the arch toward the elongate neural spine (Fig. 5D).

The vertebral centra are small, approximately 1 cm in length. They are deeply amphicoelous (Fig. 5D). The centra are spool-shaped, but not visibly keeled. The ventral edges of the anterior and posterior articular surfaces do not demonstrate distinct emarginations for the reception of intercentra.

A dorsal portion of a scapular blade, CM 34578 (Fig. 5E), demonstrates no significant diagnostic features, but is assigned tentatively to *Ianthasaurus*, primarily on the basis of appropriate size. The dorsal border is flared more than in larger species of *Edaphosaurus* (Romer and Price, 1940), a condition somewhat more similar to the rectangular shape in *Ianthasaurus* (Reisz and Berman, 1986).

Left and right femora (CM 34579 and 34581, respectively) of subequal size are assigned to *Ianthasaurus*, but only the nearly complete left one (Fig. 5F, G) forms the basis of the description here. The proximal and distal ends of the right femur are incomplete. The femoral shaft is a slender cylinder with no apparent curvature. The proximodorsal surface has a prominently developed tubercle for attachment of the puboischiofemoralis internus muscle. The relatively large size of the rugosity and its extension toward the posterior margin of the proximal head indicates that it may have also provided attachment for the ischiotrochantericus muscle. Loss of some of the surface bone from the distodorsal surface makes interpretation difficult, but it appears that the intercondylar fossa did not reach far up the shaft. Ventrally, the intertrochanteric fossa is deep and extends well down the body of the femur as in other edaphosaurs (Romer and Price, 1940). A sharp, distinct adductor ridge runs the length of the ventral surface, and its proximal terminus is marked by a broadly expanded internal trochanter for attachment of a portion of the puboischiofemoralis externus muscle (Romer, 1922; Sumida, 1989a). The distal popliteal area is a shallow concavity. A conspicuous depression on the posterior face of the posterior femoral condyle designates the proximal fibular articulation.

A complete left astragalus, CM 34580 (Fig. 5H, I), is unusually large compared to the other edaphosaurid elements from Badger Creek. Its extremely elongate proximal process, however, precludes assignment to any other taxon and has been proposed as characteristic of *Edaphosaurus* by Romer and Price (1940). It is L-shaped as in many primitive amniotes (Schaeffer, 1941). The proximal process accounts for 45% of its proximodistal length. The anterior and posterior margins of the proximal process are thickened, the latter more so for articulation with the calcaneum. The proximal surface is expanded similarly for articulation with the fibula. The dorsal surface is dominated by a large, anterodorsally facing, heart-shaped articular surface for the tibia. A conspicuous notch in the posterior edge is for the perforating artery, and a furrow-like continuation of the notch is visible

across the posteroventral surface. Just distal to the furrow is a deep pit of unknown function.

The posterior fragment of a right maxillary, CM 34449 (Fig. 5A), is assigned very tentatively to *Ianthasaurus*. Over half of the dorsal lateral surface is marked by a depressed sutural scar, consisting mainly of parallel ridges and grooves that tend posterodorsally. This marks the area overlapped almost entirely by the lacrimal and possibly in small part by the jugal. Below this the external surface sculpturing consists of irregular pits and ridges. Seven teeth are visible in lateral view, and posterior to them are the bases for the last three of the series. The remaining centimeter of the ventral margin of the maxilla just posterior to the last tooth base is smoothly rounded and did not bear any teeth. The teeth are similar to those in *Edaphosaurus* in being somewhat stout, bulbous, and isodont and in exhibiting no signs of curvature. On the other hand, in *Ianthasaurus* the marginal series consists of numerous, slightly recurved, sharply pointed teeth, with distinct caniniform teeth in the maxillary series (Reisz and Berman, 1986; Modesto and Reisz, 1990b). However, evidence of only the last ten teeth are preserved on CM 34449, and without the anterior half of the series, it is impossible to know whether caniniform teeth were present. Yet, the absence of a shelf-like structure on the lingual surface seen in well-preserved marginal teeth of *Edaphosaurus* argues for the tentative assignment of CM 34449 to *Ianthasaurus*.

Family Edaphosauridae

New but unnamed genus and species

Materials.—CM 47699 (formerly UCLA VP 1742), single dorsal neural spine (Fig. 6).

Description.—The edaphosaurid affinities of a neural spine (CM 47699, Fig. 6) are almost undeniably established by the presence of characteristic lateral tubercles, yet other features clearly separate it from other members of the family. The spine is uniformly flattened laterally, maintaining essentially the same transverse width (approximately 1.9–2.0 mm) throughout its length. It expands gradually anteroposteriorly from a narrow base of 4.5 mm to 10.7 mm at its preserved distal end. The distal tip of the spine is chipped, reducing somewhat the actual anteroposterior measurement. The lateral tubercles are hemispherical in shape, with the most proximally placed ones projecting as much as 1.5 mm beyond the lateral surface of the spine. Some of the more distally positioned tubercles are only weakly developed. Unlike many other edaphosaurids, none of the lateral tubercles are arranged in bilaterally symmetrical pairs.

Peabody (1957) erected a new species of *Edaphosaurus*, *E. ecordi*, from the Late Pennsylvanian Garnett Quarry of eastern Kansas, on the basis of a blade-like neural spine with tubercles. Vaughn (1972) identified the Badger Creek specimen as belonging to this species, noting that the two spines are strikingly similar in both shape and size. Reisz et al. (1982) argued, however, that the lateral tubercles of the holotype of *E. ecordi* are artifacts of preservation and redescribed the spine as representing a new pelycosaurian taxon, *Xyrospondylus*. Reisz and Berman (1986) have since pointed out that the primitive edaphosaur *Ianthasaurus* does not carry lateral tubercles on all of its neural spines. Thus the possibility is raised that CM 47699 could pertain to *Xyrospondylus* and that the presence or absence of tubercles reflects regional differences in the vertebral column. However, the assumption of such a generic association between isolated specimens so geographically separate would not be prudent.

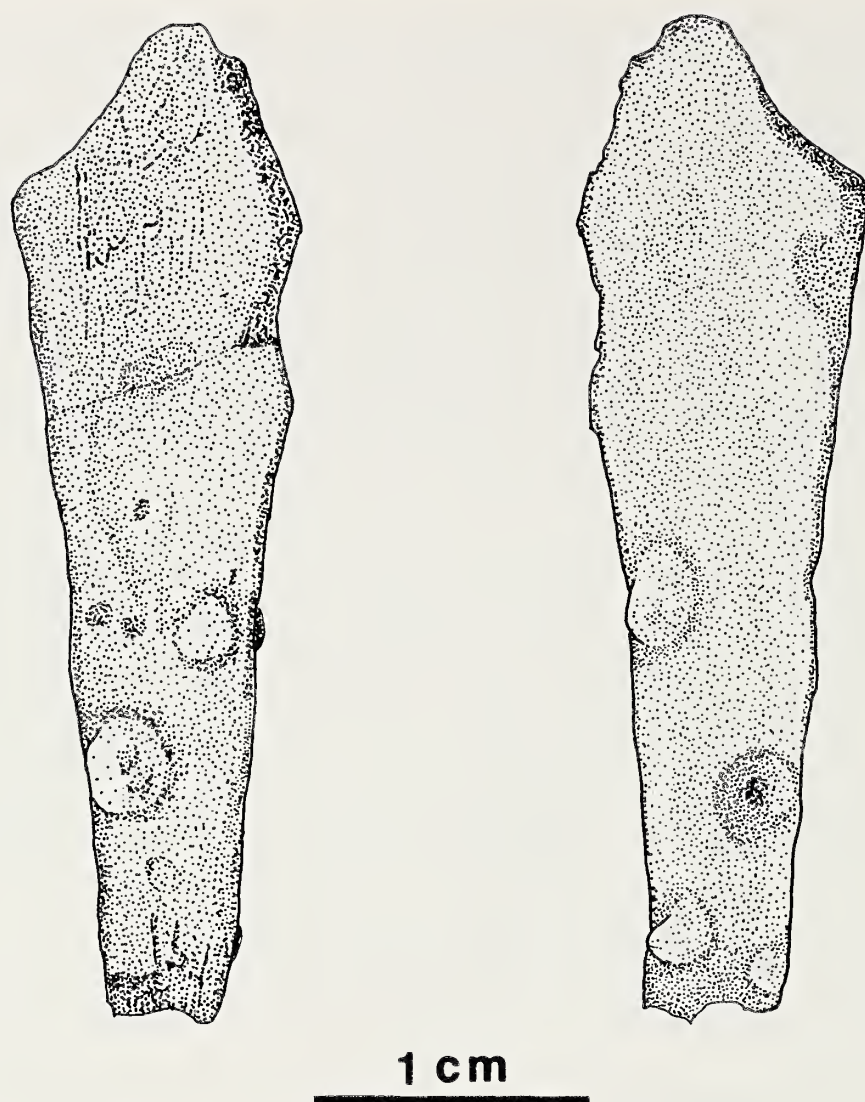


Fig. 6.—Lateral views of dorsal neural spine CM 47699 of new, but unnamed genus and species of edaphosaurid.

The entire column in *Ianthasaurus* is known (Reisz and Berman, 1986; Modesto and Reisz, 1990b), and nowhere does it exhibit blade-like neural spines. Sumida (1989b) assigned the enigmatic genus *Lupeosaurus* to the Edaphosauridae, but the neural spines of its high dorsal sail are essentially circular in cross section and lack lateral tubercles. The large, numerous, Lower Permian *Edaphosaurus* species from Texas demonstrate a tendency toward progressive increase in overall size and anteroposterior expansion of the neural spine tips of the cervical and anteriormost dorsal region to become club-like through time (Romer and Price, 1940). Additionally, there is a concomitant tendency for the spines of this region to exhibit a pronounced anterior curvature. In contrast, the spine CM 47699 increases steadily in anteroposterior dimension distally and is straight throughout its length. On the balance, the spine is unique among known members of the family and, therefore, likely represents a new species. However, because of the very limited material at hand, it would be unwise to erect a new genus and species. More conservatively, the presence of a second type of edaphosaur at Badger Creek is recognized, but erection of a new taxon should await discovery of more complete materials.

DISCUSSION

Although most Pennsylvanian-aged ophiacodonts have been assigned commonly to the genus *Clepsydraps*, it is a poorly defined genus. Despite the presence

of claw-like distal phalanges, the remainder of the limb elements of the Badger Creek ophiacodontid are essentially indistinguishable from *Ophiacodon*, and assignment to that genus could have been made with some confidence. In that regard, it is noteworthy that an as yet undescribed ophiacodont from the Garnett quarry (Reisz, 1990) also possesses claw-like distal phalanges.

More precise classification of the Badger Creek sphenacodontine cannot be justified on the basis of the materials at hand. It is worth noting, however, that this identification, if correct, marks the earliest known occurrence of this otherwise Early Permian group. The presence of a haptodontine at Badger Creek is also significant in adding to the number of rare occurrences of the subfamily in North America. In fact, Lewis and Vaughn (1965) viewed the presence of a haptodontine in the North American Lower Permian Cutler Formation of central Colorado as so unexpected that they designated it as a new genus, *Cutleria*. The Missourian age of the Badger Creek quarry provides the earliest record of the Haptodontinae in North America.

Edaphosaurs are among the most common pelycosaurs in Pennsylvanian-age faunas. Edaphosaurs have been documented from the Conemaugh and Monongahela groups of the tri state area of eastern North America (Case, 1908; Berman, 1979), as well as from a variety of locations in eastern Kansas (Reisz and Berman, 1986; Schultze and Chorn, 1988; Chorn and Schultze, 1990; Modesto and Reisz, 1990b). With one exception (Berman, 1979), Pennsylvanian records of edaphosaurs have been invariably of very small animals only a meter or so long and considerably smaller than the later forms of the Lower Permian. This is true of the more common Badger Creek form that possesses spines with typical subcircular cross section. It is potentially distinguishable from *Ianthasaurus* from the Garnett locality only on the basis of the more complete ossification of appendicular elements. In terms of absolute numbers, *Ianthasaurus* accounts for the majority of pelycosaurian materials at Badger Creek.

All of the Badger Creek pelycosaur specimens consist of isolated and often incompletely preserved bones. Thus, it is not surprising that this locality yields numerous specimens that are very probably pelycosaurian, but for which more precise taxonomic identifications are unsafe or impossible. Nevertheless, these elements are worth noting, as they further testify to the large pelycosaurian component of the quarry. All the bones are catalogued under a single number, CM 34582, despite the fact that they undoubtedly represent several taxa. Most notable are the fragmentary remains of vertebrae, scapulae, a clavicle, and humeri. Also present are tarsal elements and sharply pointed, claw-like distal phalanges.

Romer and Price (1940) and Reisz (1972, 1980, 1986) have argued that pelycosaurian-grade synapsids have diversified considerably by the Late Pennsylvanian. The presence of five distinct pelycosaurs at the Badger Creek locality provides evidence to support this contention. With the exception of the potentially new edaphosaurid taxon, the materials on which each of the taxonomic identifications were made are in general quite similar to other Late Pennsylvanian and Early Permian representatives of their respective taxa. As Reisz (1980) pointed out, the general features of most pelycosaurian families were established well before the time of the more commonly preserved Permian pelycosaurs.

The presence of five different pelycosaurs at Badger Creek ranks it among the most diverse assemblages of Pennsylvanian-aged pelycosaur localities in the world (see Table 1). Among North American localities it is surpassed in numbers of pelycosaurs only by El Cobre Canyon in northern New Mexico. Although the

exact age of the exposures from which pelycosaurs have been recovered in El Cobre Canyon is uncertain, Berman et al. (1987) have demonstrated that they are clearly Upper Pennsylvanian. An equal number of pelycosaurs has been reported from the somewhat younger Pennsylvanian locality of Garnett, Kansas (Reisz, 1990). Though the preservation of the material from Garnett is considerably better than that from Badger Creek, the latter deposit nonetheless adds to our knowledge of the distribution of early pelycosaurs. Late Pennsylvanian localities producing significant remains of tetrapods tend to be clustered about the equatorial plane of that time (Milner and Panchen, 1973; Lombard and Sumida, 1992). In this regard, Badger Creek is among the westernmost localities of undoubted Pennsylvanian age to produce pelycosaurs in North America.

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JACHAKALA: A NEW ARCHAEOLOGICAL COMPLEX OF THE
DEPARTMENT OF ORURO, BOLIVIAMARC BERMANN¹

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ABSTRACT

The chronological relationship between the pre-Hispanic Tiwanaku state and the Wankarani complex has long been unresolved. Recent research at the site of Jachakala, Bolivia, has revealed a previously unknown Tiwanaku-contemporary archaeological complex that may have succeeded the Wankarani complex in the La Joya area, Department of Oruro. This report presents a description of the pre-Hispanic occupation at Jachakala and a local ceramic sequence for the ca. A.D. 600–A.D. 1200 period.

INTRODUCTION

The Tiwanaku state has long been recognized as one of the great civilizations of the pre-Hispanic Andes. Recent investigations have revealed much about life in the Tiwanaku heartland near Lake Titicaca, but almost nothing is known of the coeval highland populations that would have been located at the southern edge of the Tiwanaku polity in what is now highland central Bolivia (the departments of La Paz and Oruro). Fragments of Tiwanaku-style pottery from sites in this region indicate contacts between the Tiwanaku polity and local populations. To date, however, there has been little investigation of these local populations, or of the nature of interaction between local populations and the Tiwanaku state.

The existing ceramic sequences for this region are based on the broadest stylistic differences in pottery from poorly documented contexts rather than systematic excavation or attempts at chronology building. As a result, although several pre-Tiwanaku (Formative) and Tiwanaku-contemporary archaeological complexes have been defined, the longevity of these complexes, and their temporal relationship to Tiwanaku have yet to be determined.

One of these Formative complexes—the Wankarani complex—represents one of the earliest village and pottery-using populations of Bolivia (Kolata, 1983). Thus studies in this poorly-known region of Bolivia are of great importance in documenting early adaptation and cultural processes in the Andean highlands. Most Wankarani complex sites are located in the southern section of the Department of La Paz and the northern part of the Department of Oruro (Ponce, 1970, 1981). Apparently a long-lived culture of great stability, the Wankarani complex persisted for many centuries. As a result of the paucity of research in this part of Bolivia, we do not yet know when the Wankarani era ended. This report presents the first description of post-Wankarani or Tiwanaku-contemporary settlement in the Wankarani area.

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Fig. 1.—Location of the La Joya research area, major Wankarani complex sites, and sites discussed in the text.

Recent research in the Department of Oruro indicates that at least some of the Wankarani sites in this area were abandoned long before the Tiwanaku polity rose to power, and that Wankarani pottery styles were replaced by a previously unknown ceramic tradition (Table 1). Survey and excavation in the canton of La Joya, Department of Oruro (Fig. 1) have recently identified non-Wankarani (but pre-Tiwanaku) and Tiwanaku-contemporary occupations at three sites. These three sites differ from neighboring Wankarani sites in site form, domestic archi-

Table 1.—*La Joya area ceramic types described in this report.*

Type clusters	Types
Jachakala Brown	Tiwanaku V
Jachakala Orange	Polychrome
Huitu Pampa Yellow	La Joya Orange
	Titina Conglomerate
	Intiraymi Mica
	Niñalupita Yellow
	Wilaque Black

tectural style, and associated pottery styles. Therefore, in the La Joya area of Oruro, we hypothesize that the Tiwanaku polity may have been interacting with a previously undescribed society that succeeded the Wankarani complex.

This report presents: (1) a description of this new complex as seen at the site of Jachakala; and (2) a preliminary ceramic sequence for the Niñalupita and Jachakala phases, respectively, the Late Formative (A.D. 500–A.D. 800) and Tiwanaku-contemporary (A.D. 800–A.D. 1200) phases in the La Joya area.

THE TIWANAKU STATE

Long known for its elaborate sculpture and massive public architecture, the site of Tiwanaku was the capital of a powerful polity between A.D. 400–A.D. 1200 (Kolata, 1983, 1986). Tiwanaku-style materials are spread over a wide area of the south-central Andes, from the *selva* to the Pacific coast of Chile and Peru. Interaction between the capital and these outlying regions apparently took several forms, ranging from direct control and colonization to indirect rule through local elites or simple trade. The least known part of the Tiwanaku sphere lies to the south of the capital; in fact, the southern edge of the Tiwanaku polity has never been defined. Exotic Tiwanaku-style trade goods are found as far south as the Atacama region of Chile (Serracino, 1980; Kolata, 1983). However, Tiwanaku-style materials have not been found in domestic contexts south of the Department of Oruro, the homeland of the Wankarani complex, one of Bolivia’s earliest archaeological cultures (Ponce, 1981).

THE WANKARANI COMPLEX

The Wankarani archaeological culture was recognized as early as the 1930s, but subsequent investigations have been limited (Métraux, 1933; Métraux and Lehmann, 1937, 1953; Condarco, 1959; López, 1959; Guerra, 1977). Named after the type site of Wankarani, located in the Department of La Paz, Wankarani complex sites are found in a broad area around Lake Poopó (Ibarra-Grasso, 1965; Walter, 1966; Ponce, 1970, 1980). Only a handful of radiocarbon dates have been run on samples from Wankarani sites. As shown in Table 3 and Fig. 2, these dates fall roughly between 1400 B.C. and 200 B.C. (Ponce, 1970).

Wankarani sites consist of isolated mounds of house remains, tombs, and occupational refuse. They range in size from 0.5–20 ha, with estimated residential populations of 80–4000 persons (Ponce, 1970, 1980:14). Ponce (1970, 1980) suggests that the sites represent semiautonomous villages linked by kin ties and common traditions, rather than a single political entity. Little is known of Wankarani adaptation, although it undoubtedly included camelid herding. The most

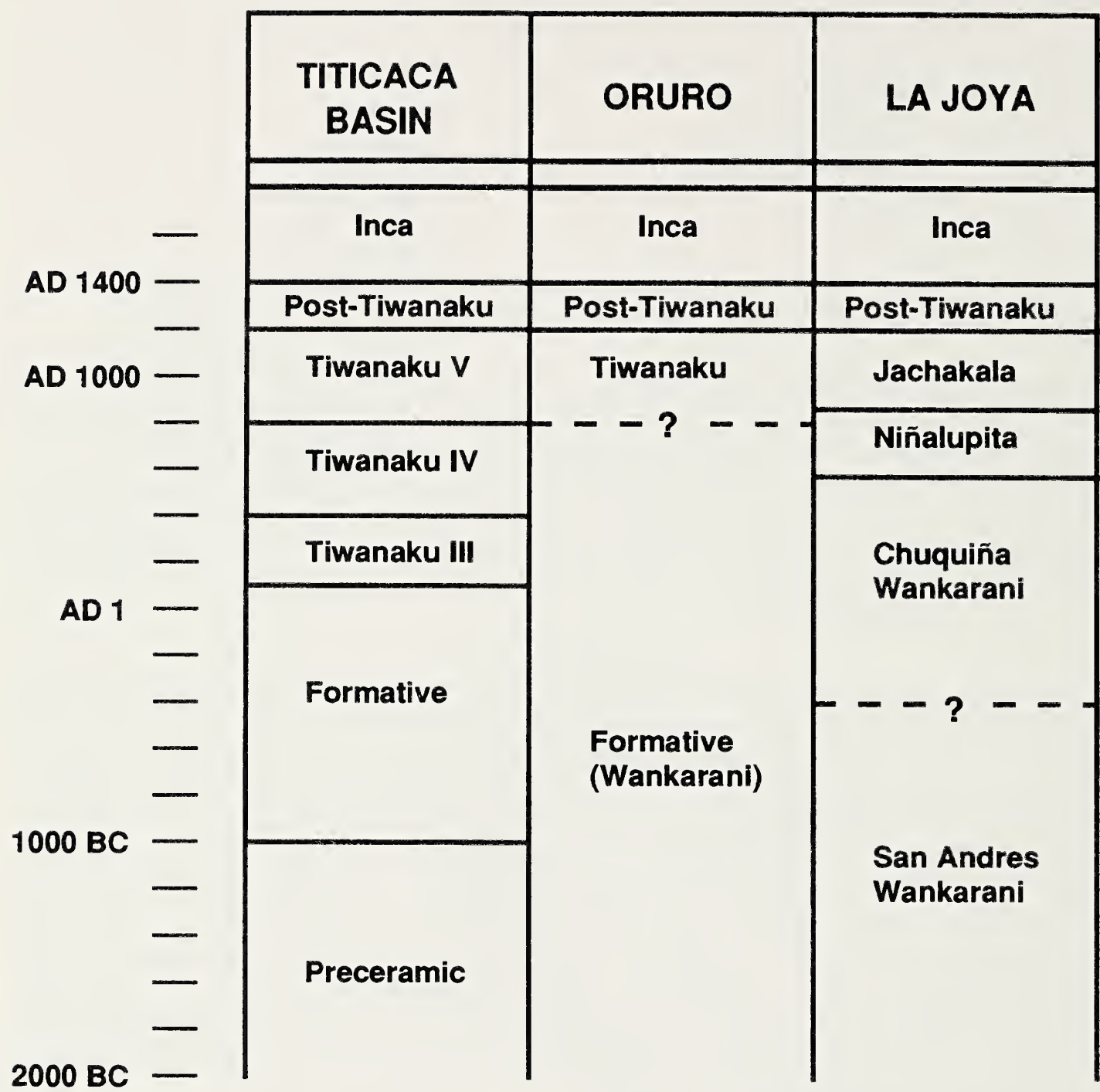


Fig. 2.—Lake Titicaca basin, Oruro, and La Joya area chronologies. This report provides a ceramic sequence for the Niñalupita and Jachakala phases.

distinctive components of Wankarani material culture are large stone sculptures of llama heads, possibly used in household ritual (Condarco, 1959; Guerra, 1977). We do not yet know when populations in the departments of La Paz and Oruro stopped producing the characteristic mound sites, round houses, stone llama heads, and pottery styles that define the Wankarani complex. In an overview of early highland Bolivia prehistory, Ponce (1970:44) reported finding pottery that shares Tiwanaku and Wankarani characteristics at a Wankarani mound near the type site. A single radiocarbon date from the nearby site of Wankarani 2 (a site with Tiwanaku-style pottery remains) yielded an uncalibrated date of 830 ± 80 B.P. (Ponce, 1981:table 1). Based on this evidence, Ponce (1970, 1981:33) hypothesized that the Wankarani complex may even have persisted until the expansion of the Tiwanaku polity late in the Tiwanaku V period

(A.D. 800–A.D. 1200). Ponce (1970:47) suggested, “Falta por fechar la superior, que se calcularía aconteció en las primeras centurias de la era christiana e inclusive su eclipsamiento total con dominio de Tiwanaku en su época V.”

THE LA JOYA AREA

In 1990 we began investigation of archaeological remains in the canton of La Joya, Province of Cercado, Department of Oruro, an area roughly 40 km east of the modern city of Oruro. Here the *altiplano*, the broad intermontane grassland plain of the south central Andes, is flat at 3720 m above sea level. The plain is only broken every 10–20 km by “*cerros*”—isolated groups of rugged hills extending as high as 500 m above the plain. Natural vegetation on the plain is sparse (*estepa montano sub tropical*), characterized by *Stipa ichu* grass, various types of cacti, small shrubs, and xerophytic grasses (Montes de Oca, 1989).

Much of the land of both the *cerros* and plain is suitable for pasturage of camelids as well as for cultivation. The current main crops, potatoes and quinoa, also may have been staples in the past. Systematic archaeological survey indicates that in pre-Hispanic times, settlement was concentrated on or around the *cerros*, as it is today.

During our regional settlement survey covering 12 km² around La Joya, we encountered six Wankarani mound sites, four sites with Tiwanaku-style pottery, and 12 Late Intermediate/Late Horizon (A.D. 1200–A.D. 1500) sites (Fig. 3). Although we might roughly order these sites into a three-part chronological sequence (Wankarani, Tiwanaku Contemporary, Late Intermediate/Late Horizon), we cannot yet be certain that differences in pottery styles reflect chronological differences. Some Wankarani sites may yet prove to have been contemporaneous with the occupation at Jachakala and other sites with Tiwanaku-style pottery.

The Site of Jachakala

Jachakala (LJ-2) was chosen as one of the sites for further investigation because of its relatively well-preserved architectural remains and the Tiwanaku-style ceramics on the surface. This site is located at the eastern foot of Cerro La Joya, roughly two km west of the Río Desaguadero, just outside the modern town of La Joya.

Jachakala does not have the mound form of Wankarani sites. Instead, it consists of architectural remains and a broad artifact scatter (320 × 210 m) spread over two large, flat, ashy areas (Fig. 4). Wall foundations from circular and rectilinear structures are visible on the surface. Most of the wall foundations consist of single alignments of unmodified field stones, but others consist of double alignments. The preserved height of most of the wall foundations is a single course of stones. In the northern section of the site are two large (14 m in diameter) stone circles of unknown function. These circles may represent large structures or corrals. To the west of the circles is a well-preserved section of stone-lined canal or drain.

Surface materials at Jachakala include fragments of pottery, projectile points, stone tool debitage, basalt axes, and a small number of grinding stones.

Our systematic surface collection at Jachakala helped define the edges of the site and explore intrasite spatial artifact patterning. Surface collection units measuring 2 × 2 m were placed at 50 m intervals across the site and all artifactual remains in each unit were collected. The amount of black basalt at the site, mostly in the form of axes or “hoes” was truly impressive (Fig. 5). An average of 30

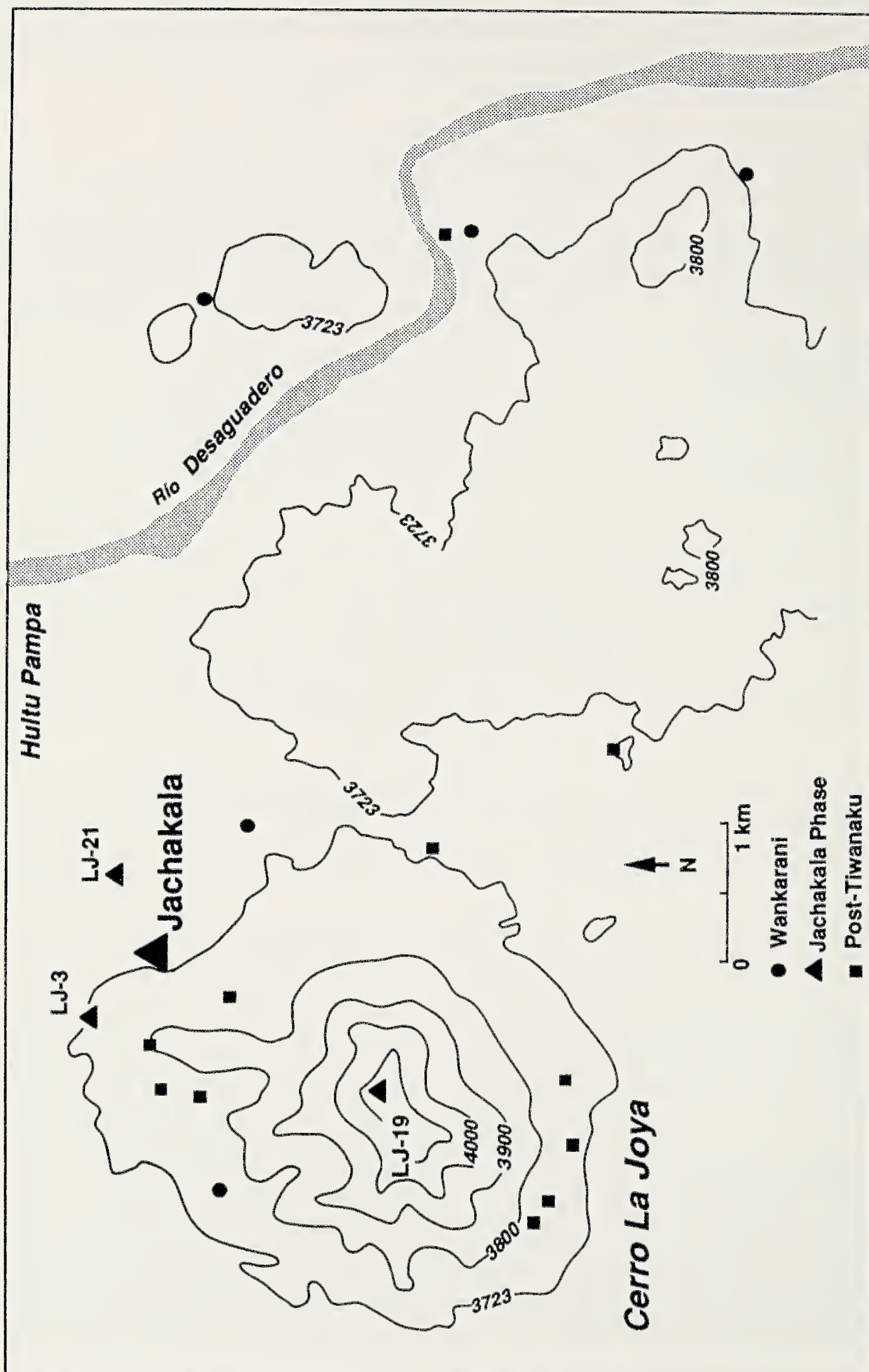




Fig. 4.—Map of Jachakala showing architectural remains visible from the surface and locations of excavation units 1 and 2.

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Fig. 3.—Sites in the La Joya research area.

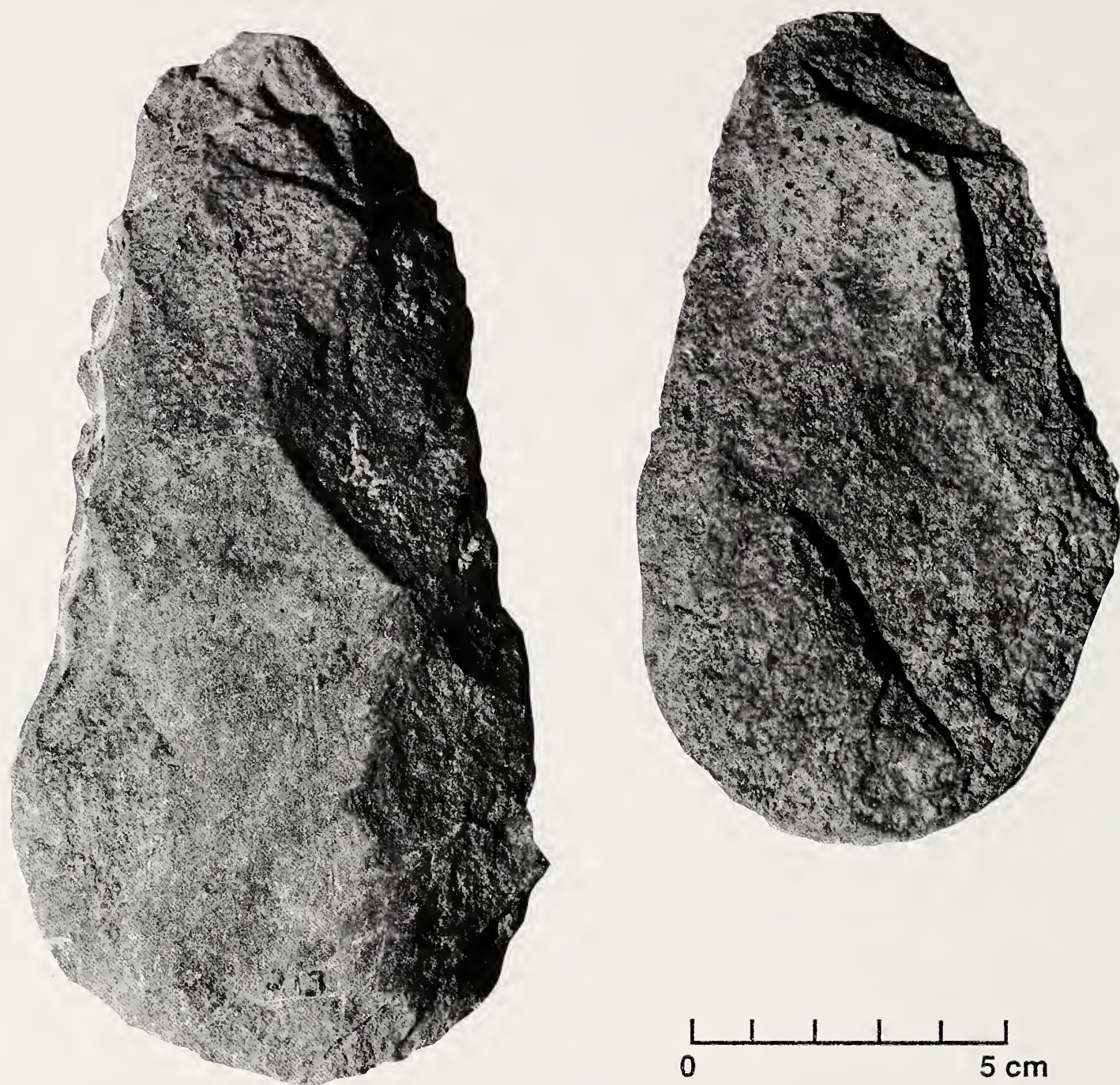


Fig. 5.—Black basalt axes from the surface of Jachakala.

basalt items, with an average weight of 3.2 kg, were found in each 2×2 m collection unit. This figure allows us to suggest a total of over 5000 kg of basalt lithics *on the surface alone* at Jachakala. With the exceptions of a handful of scrapers, blades, and projectile points, all the basalt tools consisted of finished axes. No large chunks of unworked basalt were found, and we do not know if the axes were being manufactured at Jachakala. The black basalt probably represents an item of long-distance trade. The nearest known basalt source is the pre-Hispanic quarry at Querimita, near Lake Poopó, some 100 km to the south (Ponce, 1981).

Preliminary analysis has not revealed any significant spatial patterns in the distribution of materials. Roughly 4% of the surface sherds were from Tiwanaku-style polychrome or black-on-red decorated vessels. The remainder of the surface sherds were from undecorated, non-Tiwanaku orangeware or grayware vessels of previously undescribed types. No Wankarani-style or Post-Tiwanaku pottery fragments were recovered from the surface.

Excavation at Jachakala

Two test pits (judgmentally placed) were excavated at Jachakala. Unit 1 was placed in a potential midden (an ashy surface area with high artifact density). Unit 2, in an area of architecture, was intended to date through ceramic associations the occupation of a circular structure visible on the surface.

Unit 1 (a 2 × 2 m-test pit) exposed a series of occupational surfaces used for mortuary activities and disposal of cooking refuse (Fig. 6). No architectural remains were found. In contrast to our expectations, the area did not prove to be a deep midden, and artifact density dropped markedly below the surface ashy layer. Below this stratum were various other layers of sandy clay, each containing a small number of artifacts. Several of these layers may represent episodes of inundation by the nearby Río Desaguadero which periodically floods its banks.

At 54–60 cm below datum, the sandy clay strata were replaced by a sequence of deposits containing higher quantities of occupational debris, including two that represent buried occupational surfaces (levels L and K). Artifacts from levels L and K included large numbers of pottery fragments, some of them red-slipped, and obsidian debitage. A small refuse pit (Feature 3) in one surface (Level K) contained the burned leg and foot (minus the toes) of a juvenile camelid. Two large stones at 45 and 55 cm below datum proved to be cap stones for unlined, bell-shaped cist tombs (features 7, 8, and 9).

The best preserved tomb (Feature 7) contained the remains of an adult buried facing to the east in a seated and flexed position, with the arms under the legs. Preservation was poor, and the sex of the individual could not be determined. The skull exhibited artificial deformation of the “tabula” style. No grave goods were found in the tomb, but the mouth of the individual contained a copper *tembete* or lip plug. This ornament is occasionally depicted in Tiwanaku portrait vessels.

At roughly 85 cm below datum the fill in Unit 1 changed once again, to a sequence of heterogeneous, silty clay layers. At the interface of this new fill and the upper strata were a small, empty pit, a large grinding stone (lying flat), and an association of camelid bone (Feature 6). Artifact density dropped sharply below 90 cm below datum, and sterile soil was reached at roughly 105 cm below datum.

The few Tiwanaku V-style pottery fragments associated with the upper occupational surfaces (levels L and K) suggest occupation between A.D. 800 and A.D. 1200. All the burials and Feature 3 are associated with these Tiwanaku V period occupations.

Unit 2 (a 1 × 3 m-trench) exposed part of a circular dwelling dating to the Tiwanaku V period. This structure exhibited two episodes of occupation or use. Below the structure were several thick deposits of ash and smaller ash lenses (Fig. 7).

The surface both inside and outside the structure consisted of a 4 cm-thick layer of loose, powdery gray ash and silt. Artifact density was high in this deposit, including sherds with badly eroded surfaces. The gray ash and silt deposit was underlain by layers of dark reddish-brown silty clay with lower artifact density. Differences between the fill inside and outside the structure began to appear at roughly 30 cm below datum. Inside the structure fragments of burned clay or adobe (wall remains?) began to appear at roughly 45 cm below datum.

A floor (Feature 2) for the structure was found at roughly 50 cm below datum, suggesting that the structure may have been slightly subterranean. The surface

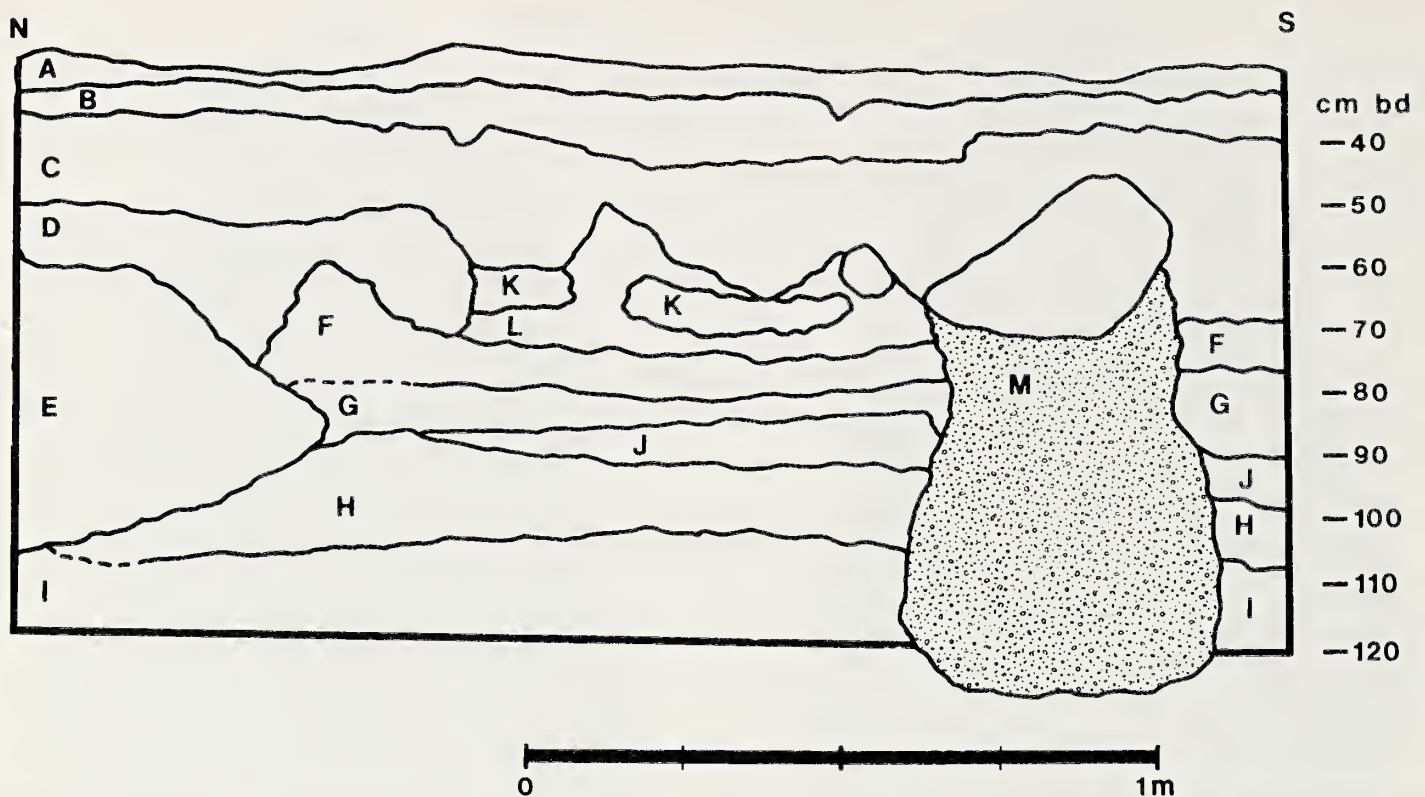


Fig. 6.—Profile of east baulk of Unit 1. Key: A, Homogeneous loose gray (10R 6/1) silty sand; fine-grained; low organic content; roots and pebble inclusions. B, Homogeneous red-brown to pink (5YR 6/3) sandy clay; compact and hard; moderate organic content; root and insect activity. C, Heterogeneous light-brown (5YR 7/3) sandy, silty clay with red-brown (5YR 6/6) patches; weak crumb structure; compact and hard; moderate organic content; no inclusions. D, Homogeneous brown (5YR 4/2) silty clay; medium granular structure; compact and hard; moderate organic content; charcoal flecks and 0.5 cm charcoal chunk inclusions. E, Slightly heterogeneous dark brown (5YR 3/4) loamy clay; weak crumb structure, possibly disturbed; compact but not hard; moderate-high organic content; charcoal chunk inclusions. F, Homogeneous reddish-brown (5YR 5/6) silty clay; well-developed platy structure; compact and hard; moderate organic content; charcoal flecks. G, Homogeneous orange-brown (5YR 5/8) silty clay; high silt and sand content; strong horizontal structures with 0.2–0.5 cm-thick microstrata; low organic content; no charcoal inclusions. H, Homogeneous orange-brown (7.5YR 5/4) silty clay; high silt and sand content; strong horizontal structures with 0.2–0.5 cm-thick microstrata; low organic content; no charcoal inclusions. I, Homogeneous dark reddish-brown (5YR 5/8) silty clay; no horizontal structure; compact and hard; low-moderate organic content; charcoal flecks. J, Homogeneous dark brown (5YR 4/4) silty clay; no horizontal structure; compact and hard; low-moderate organic content; few charcoal flecks. K, Heterogeneous silty loam ash ranging from light gray (5YR 6/1) to white; loose, powdery, and soft; very high organic content; pebble, charcoal fleck, and charcoal chunk inclusions; occupational surface. L, Homogeneous reddish-brown (5YR 4/6) silty clay; compact and hard; moderate organic content; charcoal flecks; occupational surface? M, Disturbed and homogeneous dark brown (2.5YR 4/2) silty clay; compact but not hard; charcoal and pebble inclusions; tomb fill of Feature 7.

consisted of a 1–2 cm-thick layer of homogeneous, light brown, compacted sand. Lying directly on this organically stained surface were fragments of charcoal, sherds, burned straw or thatch, lithic debris, a worked bone scraper, and animal bone. A posthole was found near the interior edge of the wall. South of the posthole was a concentration of camelid bones in a shallow pit.

This floor was underlain by a 5–6 cm-thick layer of wall-melt: a very dark gray clay, mixed with pebbles and charcoal flecks. Under this was a second surface or floor (Feature 4) at roughly 68 cm below datum. This floor consisted of a light brown sandy surface, but was cleaner, with less staining, than the upper floor. There were fewer artifacts than on the upper floor: some plainware sherds, bone fragments, and a small obsidian projectile point. No features were found. In

summary, the stratigraphy suggests two episodes of occupation, or that after abandonment and decay, the structure was used as an activity area (represented by the upper occupational surface).

The deposits outside the wall were very different below the uppermost stratum. An ashy midden began to appear at 45 cm below datum, consisting of thick ash lenses separated by layers of silty clay. The ash deposits found outside the house clearly predate the occupation of the house. A single charcoal sample (Pitt-1118) from one of the ash lenses provided an uncalibrated date of 1350 ± 40 B.P., suggesting a midseventh century occupation (see Table 3). Most of the ash deposits represent secondary deposition rather than in situ burning, but a small firepit (Feature 5) was found at roughly 110 cm below datum, containing a small amount of ash and carbon. Unfortunately a carbon sample (Pitt-1119) taken from the firepit provided a modern date (Table 3). Artifact density was fairly high in most of the ash lenses as well as in the layers of silty clay. Artifacts included fragments of fire-blackened utilitarian pottery, animal bones, and basalt stone flakes and debitage. Fragment of burned adobe with *paja* impressions were found at 60–63 cm below datum. One of these bore traces of red pigment, suggesting that the house walls had been decorated. Several specimens of slag from copper smelting were found near the base of the excavation at roughly 135 cm below datum. The unit was not excavated to sterile soil.

Artifact density was highest between 112 and 120 cm below datum (strata JJ and FF): Level 11 yielded 160 ceramics, 186 animal bone fragments, and 13 lithics—or roughly 4800 artifacts per m^3 . In contrast, the mean artifact density for the deposits outside the structure was 2200 per m^3 .

THE JACHAKALA POTTERY ASSEMBLAGE

The main goal of the analysis of the Jachakala ceramic assemblage was to begin forming a regional ceramic chronology. Preliminary analysis of the survey and surface collection from other sites is not yet complete. Therefore this report focuses on the excavated material from units 1 and 2 at Jachakala. The ceramic lots used in the analysis include levels 1–10 of Unit 1, levels 1–6 inside the structure, and levels 7–15 outside of the structure of Unit 2. A total of 1884 excavated sherds was used in the analysis.

Ceramic Types

Excavation and surface collection allowed preliminary classification of a set of plainware pottery types used at Jachakala and the nearby site LJ-3 (Table 1). Many of the plainware pottery types continued in use after Tiwanaku-style pottery appeared. Because these plainware types are not found at Tiwanaku, at Tiwanaku regional sites, nor at nearby Wankarani sites, we can treat them as an indigenous ceramic tradition. Examples of these new types are illustrated in Fig. 8–10, and classificatory descriptions are given in Appendix I.

On the basis of diachronic changes in the Jachakala pottery assemblage, we have defined two phases: the Niñalupita Phase (before Tiwanaku V-style pottery began to arrive at Jachakala), and the subsequent Jachakala Phase (when Tiwanaku V-style pottery was used in Jachakala households).

A type-variety classification system was used in preliminary analysis of the Jachakala pottery remains. Details of this analysis are presented in Appendix I. In general, sorting of sherds on the basis of temper, paste composition, surface

finish, and decoration attributes led to the creation of the several distinct types and the less well-defined "type clusters" listed in Table 1.

Mica-tempered sherds that could not be identified as La Joya Orange, Intiraymi Mica, or Niñalupita Yellow (Fig. 9a–e) were classified as Jachakala Brown or Jachakala Orange depending on paste color. Jachakala Brown and Jachakala Orange ceramics thus exhibited a great deal of variation in temper and finish characteristics, and represent "type clusters" rather than true types. Sherds without mica temper included Titina Conglomerate (Fig. 9) and the "type cluster" Huitu Pampa Yellow. Several of the types are based on relatively small numbers of sherds, and the typology will be modified as the research continues.

The seriation shown in Fig. 11 is based on this ceramic classification and stratigraphic context. Comparison of the ceramic assemblage from each level

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Fig. 7.—Profile of south baulk of Unit 2 showing position of house floors (strata F and H). Key: A, Homogeneous gray (5YR 6/2) sandy, silty; loose, granular; pebbles and roots. B, Homogeneous gray-brown (7.5YR 6/4) silty clay; moderate sand content; compact and hard; faint horizontal structure; root activity. C, Heterogeneous gray (2.5YR 5/6) silty clay with horizontal microstrata; compact but not hard; moderate organic content. D, Slightly heterogeneous light brown (5YR 5/3) silty, loamy clay; compact and hard; weak granular structure; moderate organic content; charcoal fleck inclusions. E, Homogeneous dark brown (5YR 4/2) silty, loamy clay; compact and hard; moderate organic content; no visible structure; pebble and charcoal inclusions. F, Homogeneous light brown (7.5YR 6/4) sandy silt; mottled; compact but not hard; moderate organic content; charcoal stained and charcoal fleck inclusions. G, Homogeneous dark brown (5YR 3/2) silty, loamy clay; compact and hard; moderate-high organic content; no visible structure; pebble and charcoal inclusions. H, Homogeneous light brown (7.5YR 6/4) sandy silt; compact but not hard; charcoal fleck inclusions. I, Homogeneous dark brown (5YR 4/2) silty, loamy clay; compact and hard; charcoal fleck inclusions. J, Homogeneous red-brown (5YR 5/6) silty clay; compact and hard; moderate organic content; horizontal microstrata; charcoal fleck inclusions. K, Heterogeneous gray-green (2.5YR 6/0) ash lens; soft and loose; moderate-high organic content; horizontal microstrata; charcoal fleck inclusions. L, Homogeneous gray (5YR 6/1) silty, sandy loam; granular structure; compact but not hard; deposits of charcoal flecks and ash at margins. M, Heterogeneous light gray (5YR 7/1) silty loam flecked with white clay inclusions; weak horizontal structure; high organic content. N, Homogeneous red-brown (2.5YR 5/4) silty clay; compact but not hard; granular; charcoal flecks at interfaces. O, Heterogeneous light red to brown-gray (10R 5/2) silty clay; no charcoal. P, Homogeneous gray-brown (10R 5/1) loamy, silty clay; high organic content; charcoal fleck inclusions. Q, Slightly heterogeneous red-brown (10R 5/3) loamy clay; compact but not hard; moderate organic content; charcoal fleck inclusions. R, Heterogeneous dark brown (10R 5/2) loamy clay; compact; ash and sand pockets; charcoal fleck inclusions. S, Homogeneous gray (7.5YR 6/0) ashy loam; soft and loose; high organic content. T, Homogeneous dark red-brown (5YR 5/4) silty clay loam; compact and hard; charcoal and root inclusions. U, Heterogeneous loose gray (10R 6/1) to dark gray (10R 4/1) ash and silt with pockets of (burned?) orange (2.5YR 6/6) clay; horizontal structure; high ash and charcoal content; base of a cultural feature (pit). V, Slightly heterogeneous gray (7.5YR 6/0) ashy loam; soft and loose; high organic content. AA, Heterogeneous light gray (2.5YR 6/0) ash and silt; compact but not hard; charcoal chunk inclusions. BB, Homogeneous gray-green (10YR 5/1) ash and silt; high organic content; charcoal chunk inclusions. CC, Homogeneous orange-brown (5YR 5/4) sandy, silty clay; compact and hard; moderate organic content; charcoal fleck inclusions. DD, Homogeneous gray-green (10YR 5/1) ash and silt; high organic content; charcoal chunk inclusions. EE, Homogeneous orange-brown (5YR 5/4) sandy, silty clay; compact and hard; moderate organic content; charcoal fleck inclusions. FF, Homogeneous orange-brown (5YR 5/4) sandy, silty clay; compact and hard; moderate organic content; charcoal fleck inclusions. GG, Homogeneous gray-green (10YR 5/1) ash and silt; high organic content; charcoal chunk inclusions. HH, Homogeneous light brown (7.5YR 6/2) ashy silt; moderate sand content; no charcoal. II, Homogeneous gray-green (10YR 5/1) ash and silt; high organic content; charcoal chunk inclusions. JJ, Homogeneous gray-green (10YR 5/1) ash and silt; high organic content; charcoal chunk inclusions. KK, Homogeneous orange-brown (5YR 5/4) sandy, silty clay; compact and hard; moderate organic content; charcoal fleck inclusions. LL, Homogeneous light red-brown (5YR 6/3) silty clay.

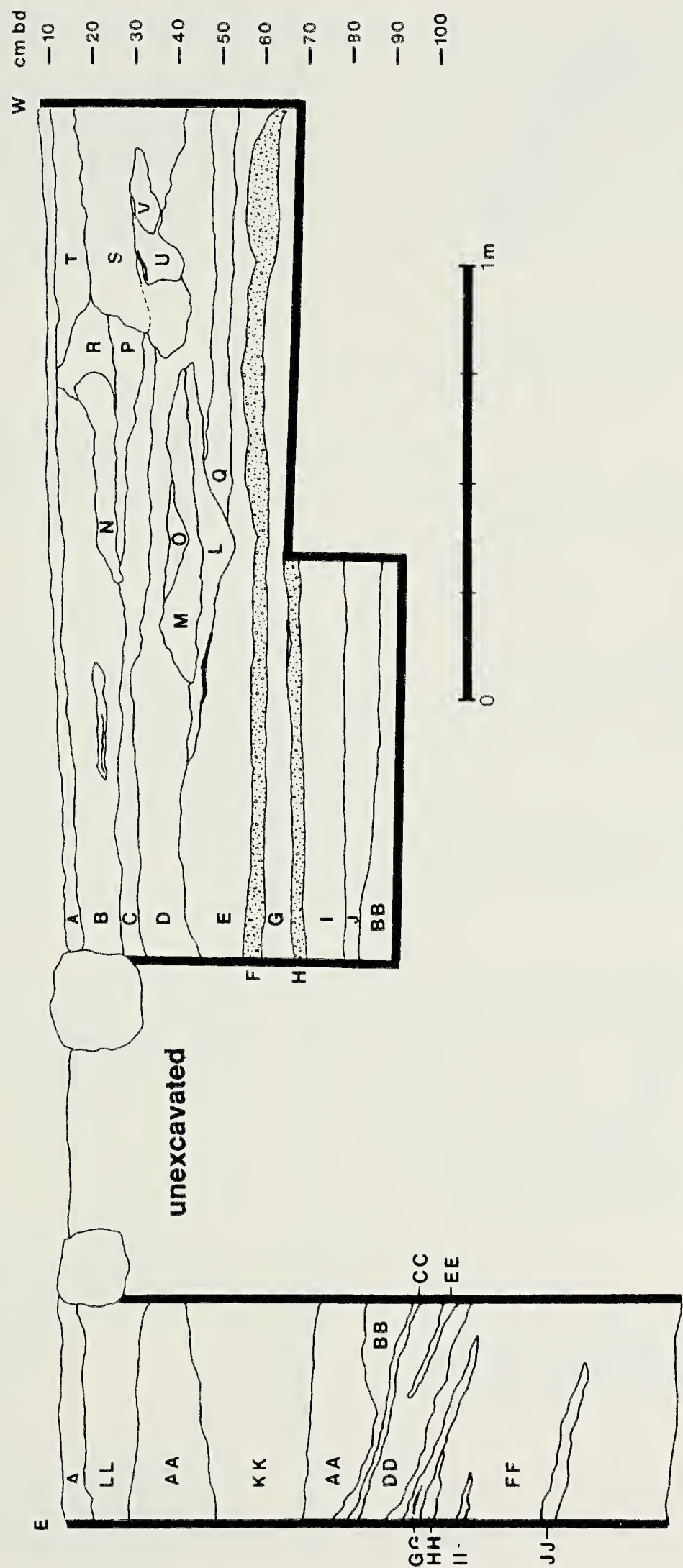


Table 2.—Frequencies (sherd counts and percentages [in parentheses] by level of ceramic types from Unit 2, Jachakala.

Level	Jachakala Brown	Jachakala Orange	Huitu Pampa Yellow	Niñalupita Yellow	La Joya Orange	Intiraymi Mica	Titina Conglomerate	Other	Total
1	6 (12)	10 (21)	32 (67)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	48
2	33 (15)	54 (25)	120 (55)	7 (3)	0 (0)	0 (0)	2 (1)	3 (1)	219
3	46 (18)	88 (34)	114 (44)	4 (2)	0 (0)	5 (2)	0 (0)	2 (1)	59
4	53 (20)	101 (38)	86 (32)	14 (5)	0 (0)	3 (1)	9 (3)	2 (1)	68
5	22 (24)	43 (48)	13 (4)	2 (2)	0 (0)	6 (7)	4 (4)	0 (0)	90
6	5 (8)	20 (32)	4 (6)	4 (6)	5 (8)	21 (34)	3 (5)	0 (0)	62
7	3 (8)	16 (40)	4 (10)	3 (8)	1 (3)	11 (28)	2 (5)	0 (0)	40
8	22 (22)	32 (31)	5 (5)	10 (10)	8 (8)	19 (19)	5 (5)	1 (1)	102
9	12 (16)	39 (52)	2 (3)	6 (8)	6 (8)	7 (9)	3 (4)	0 (0)	75
10	7 (12)	30 (52)	3 (5)	5 (9)	6 (10)	5 (9)	2 (3)	0 (0)	58

Table 3.—Radiocarbon dates from Jachakala and the Wankarani sites of Wankarani, Sokotiña, and San Andres. Calibrations using Stuiver and Pearson, 1986 and Pearson and Stuiver, 1986.

Site	Lab #	Radiocarbon years B.P.	Calibrated years B.C./A.D.	Calibrated range B.C./A.D.	Reference
Wankarani	Hv-121	2750 ± 100	905	1005–815	Wendt et al., 1962
Wankarani	Gak-1037	3160 ± 110	1435	1525–1310	Ponce, 1970
Wankarani	Gak-1038	2200 ± 80	310,325,355	385–170	Ponce, 1970
Wankarani	Gak-1039	2300 ± 80	390	405–360	Ponce, 1970
Sokotiña	P-1134	3098 ± 60	1405	280–255	Stukenrath, 1967
San Andres	B-55309	2970 ± 90	1221,1240,1255	1435–1315	
San Andres	B-55310	2850 ± 130	1010	1390–1040	
San Andres	B-55311	3930 ± 240	2465	1260–900	
San Andres	Pitt-1120	50 ± 145	modern	>2490–2130	
Jachakala	Pitt-1119		modern		
Jachakala	Pitt-1118	1350 ± 40	665	645–680	

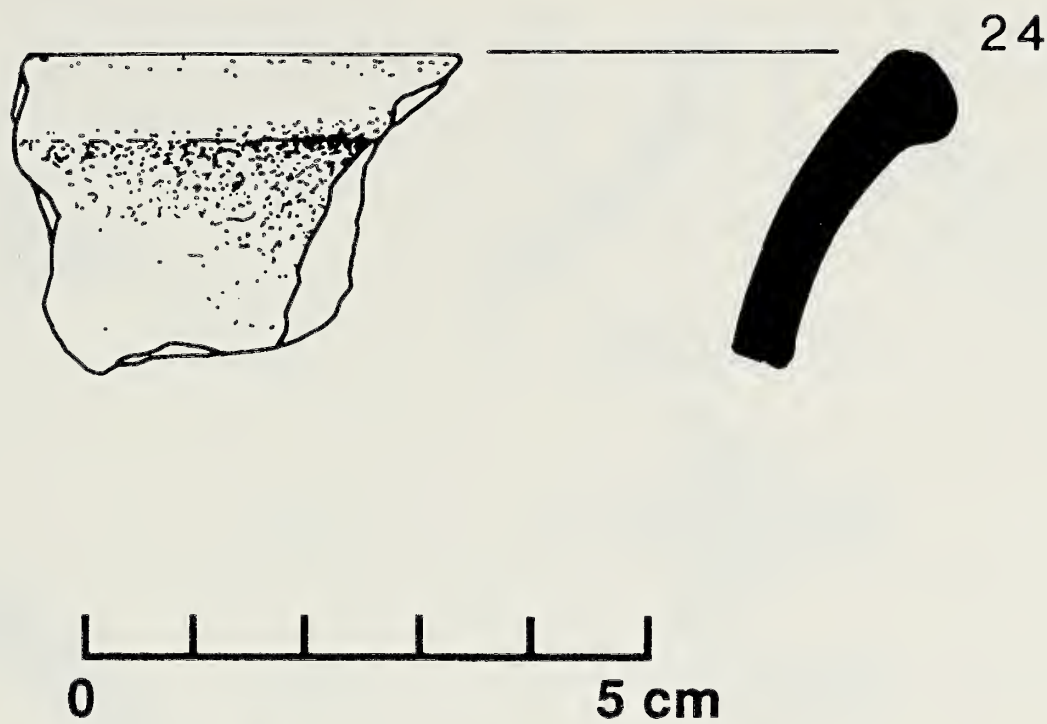


Fig. 8.—La Joya Orange rim from Unit 2.

revealed several diachronic trends that form the basis for the Jachakala ceramic sequence (Table 4).

The proportion of non-mica tempered pottery increased dramatically through time at Jachakala. As shown in Fig. 11, Huitu Pampa Yellow (the most common non-mica temper type cluster) grew from 0.5% (in Level 10) to over 65% (in Level 1) in Unit 2. There was also a significant increase in total sherds without mica temper between levels 5 and 4 (Fig. 12; Table 2).

Small quantities of Tiwanaku-style materials were found below the structure partially exposed in Unit 2. The deepest occurrence of Tiwanaku-style materials were three sherds from Level 7, below the lower floor of the structure, at 80 cm below datum.

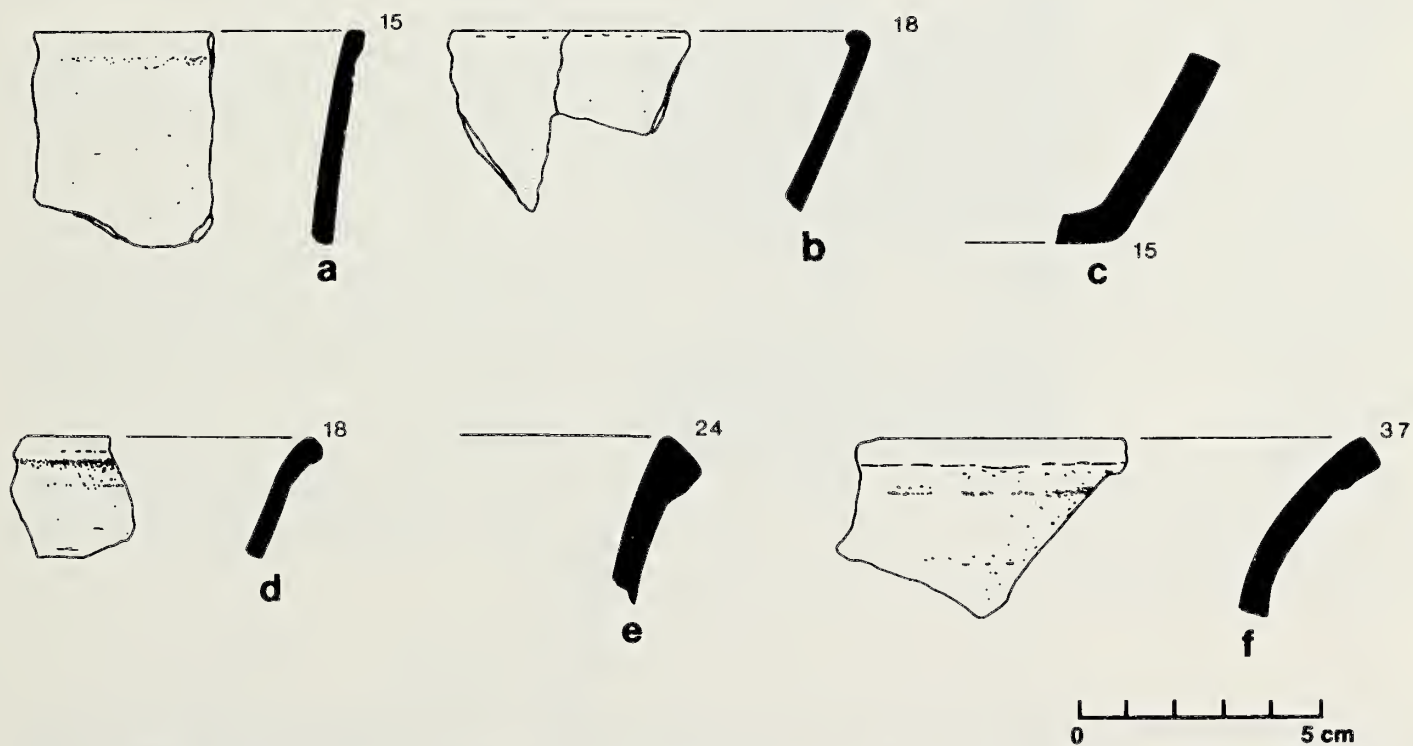


Fig. 9.—Niñalupita fragments (a–e) and Titina Conglomerate rim (f) from Unit 2.

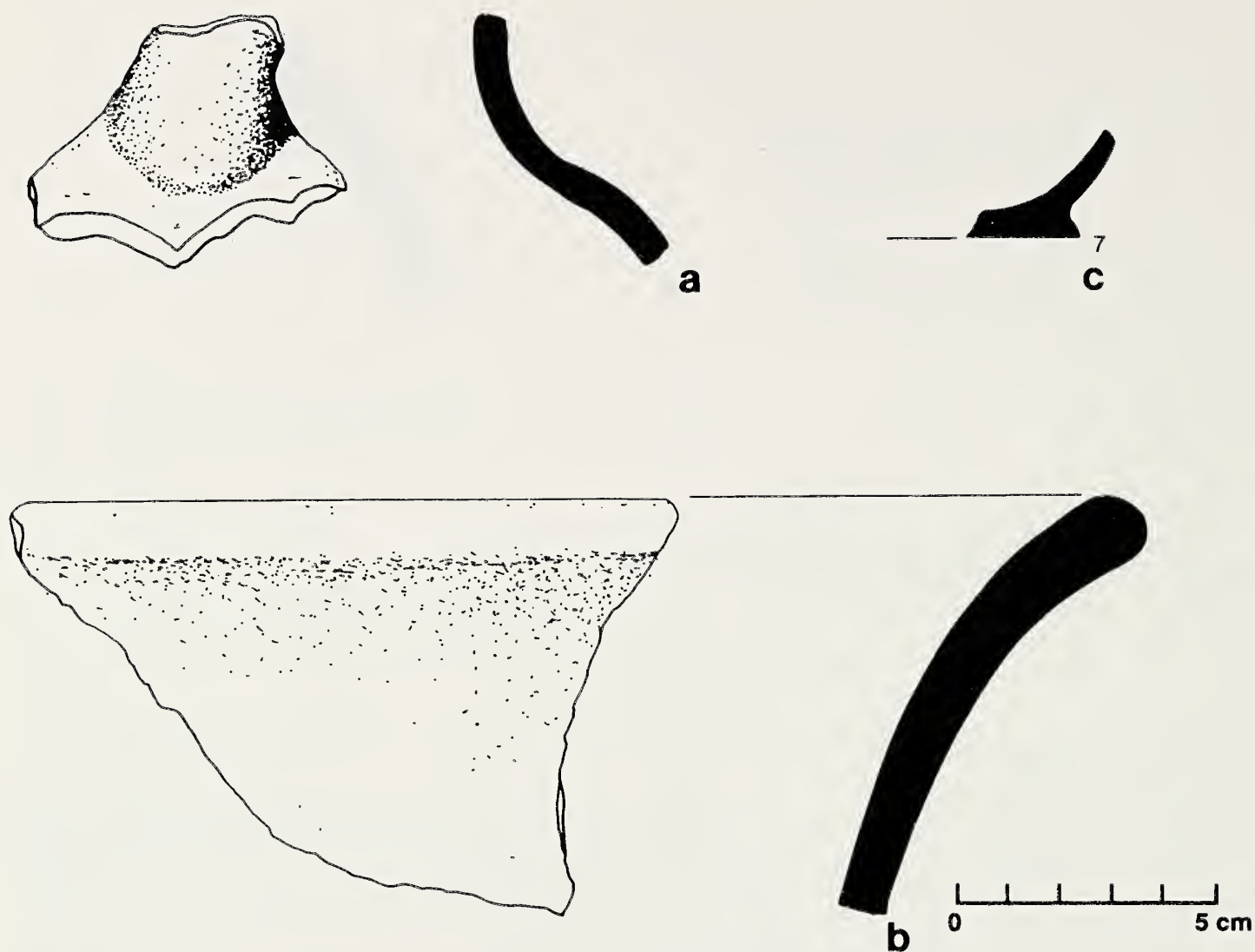


Fig. 10.—Wankarani pottery. These fragments of Wilaque Black are from the surface of the site of Wilaque.

La Joya Orange (Fig. 8) was not found above 35 cm below datum in either excavation. As shown in Fig. 11, the proportion of La Joya Orange increased with depth from 9% to 15% of the total ceramic assemblage.

Fragments of Titina Conglomerate (Fig. 9f) were most frequent between 90 and 115 cm below datum. Although never more than 6% of the total assemblage, Titina Conglomerate fragments made up more than 40% of the non-mica tempered ceramics in levels 6, 8, and 9.

Intiraymi Mica represents another early pottery type in the Jachakala assemblage. This type was only found below 30 cm below datum in both excavations. The frequency of Intiraymi Mica fragments increased with depth, peaking between 70 and 90 cm below datum, and constituting 38% of the total ceramic assemblage in Level 6.

Niñalupita Yellow (Fig. 9a–e) ceramics were found only in Unit 2 at Jachakala. They were recovered from each excavation level of Unit 2 except the uppermost one. Generally, Niñalupita Yellow made up a minor proportion of the overall ceramic assemblage, ranging from 3–9% over time.

Tiwanaku-Style Pottery at Jachakala

Ceramics associated with both floors exposed in Unit 2 indicate that the structure dates to the Jachakala Phase or Tiwanaku V period (A.D. 800–A.D. 1200).

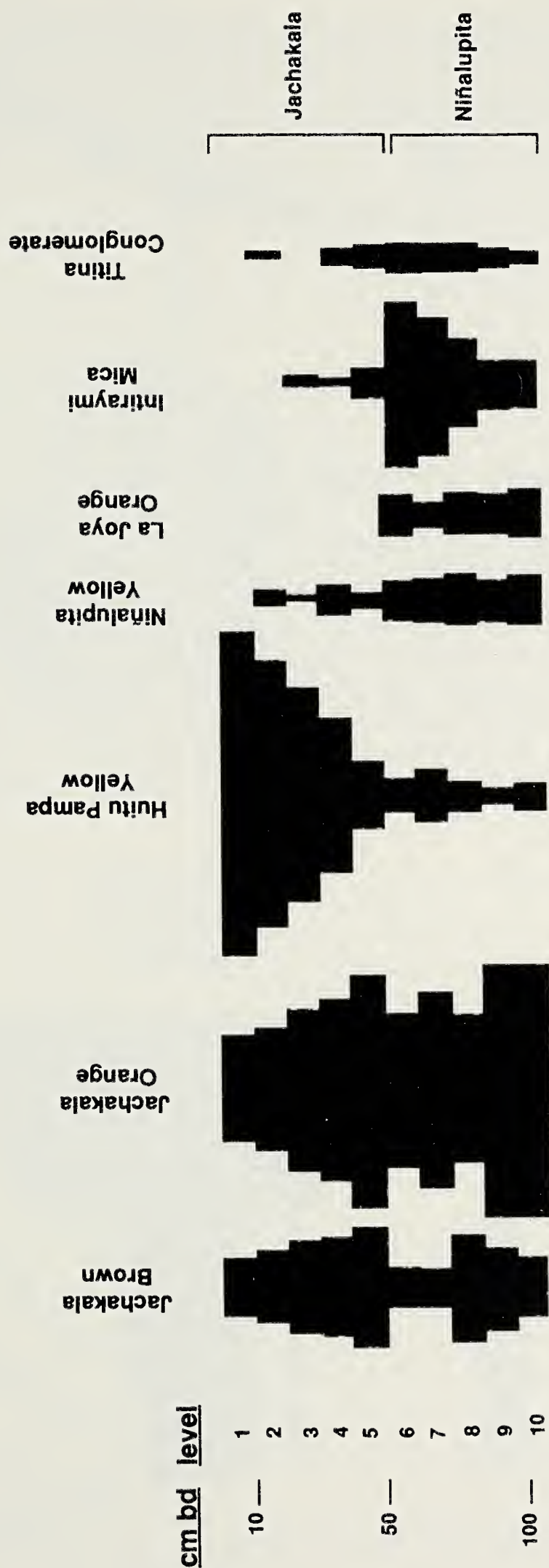


Fig. 11.—Relative proportions by level of ceramic types from Unit 2, Jachakala. Each level corresponds to roughly 10 cm.

Table 4.—Frequencies by level of sherds without mica temper from Unit 2.

Level	Nonmica temper (ct)	Total sherds	% of Total sherds without mica temper
1	32	48	66.6
2	125	219	57.1
3	116	259	44.8
4	97	268	36.2
5	17	90	18.9
6	7	62	11.3
7	6	40	15.0
8	11	102	10.8
9	5	75	6.7
10	5	58	8.5

Fragments of Tiwanaku V-style pottery were found in both the floor contact zones and in the layer directly below the lower floor.

Only a fraction of the Tiwanaku V pottery assemblage known from Tiwanaku is represented at Jachakala (or other La Joya sites). All of the decorated Tiwanaku-style ceramics at Jachakala are from polychrome and black-on-red/orange *keros* and flaring-sided bowls (Fig. 13 and 14). The only Tiwanaku-style undecorated pottery represented at Jachakala is punctate necklace vessels, a common Tiwanaku IV and V period plainware form found at many Tiwanaku sites (Bennett, 1934; Bermann, 1990). Fig. 15 shows a diagnostic neck fragment from one of these vessels. Fragments of the Tiwanaku V *puma incensarios*, polished blackware vessels, or pitcher forms that are common at regional Tiwanaku sites in Peru,

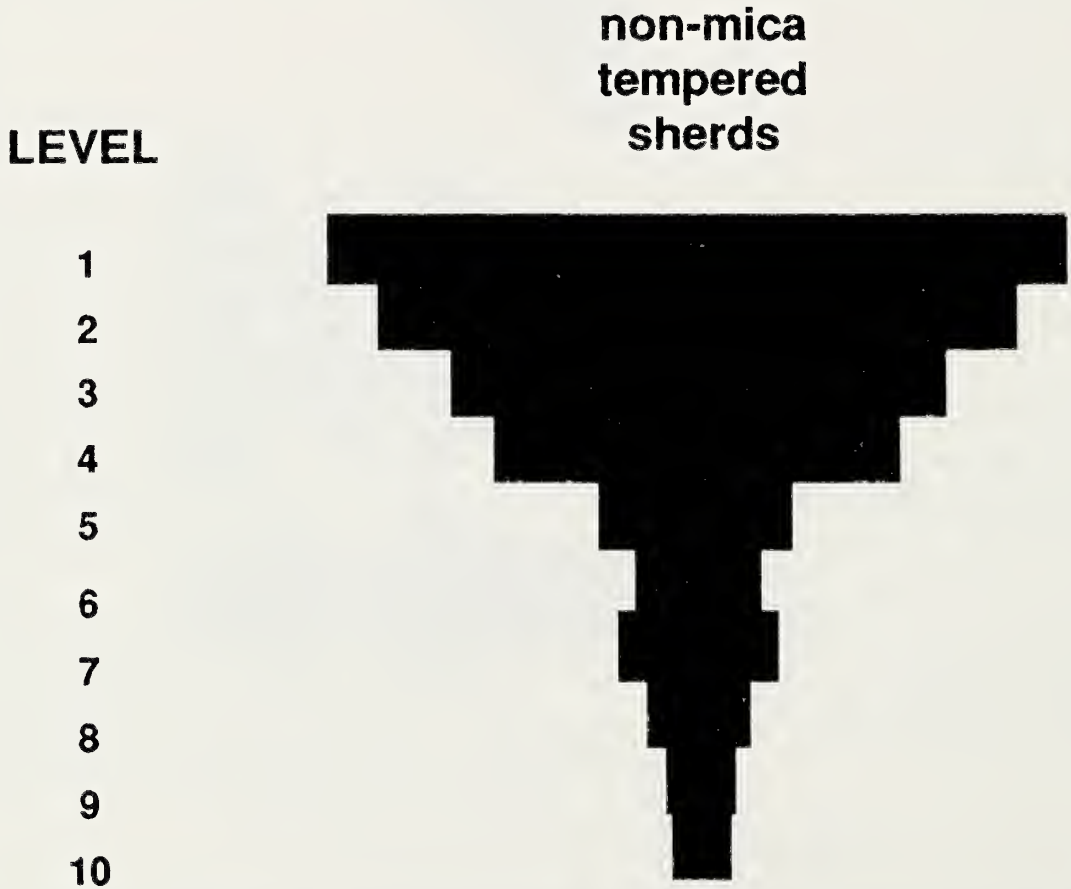


Fig. 12.—Relative proportion by level of pottery without mica temper pottery from Unit 2, Jachakala.



Fig. 13.—Tiwanaku V-style *kero* (a) and *kero* fragment (b) from the surface of Jachakala.

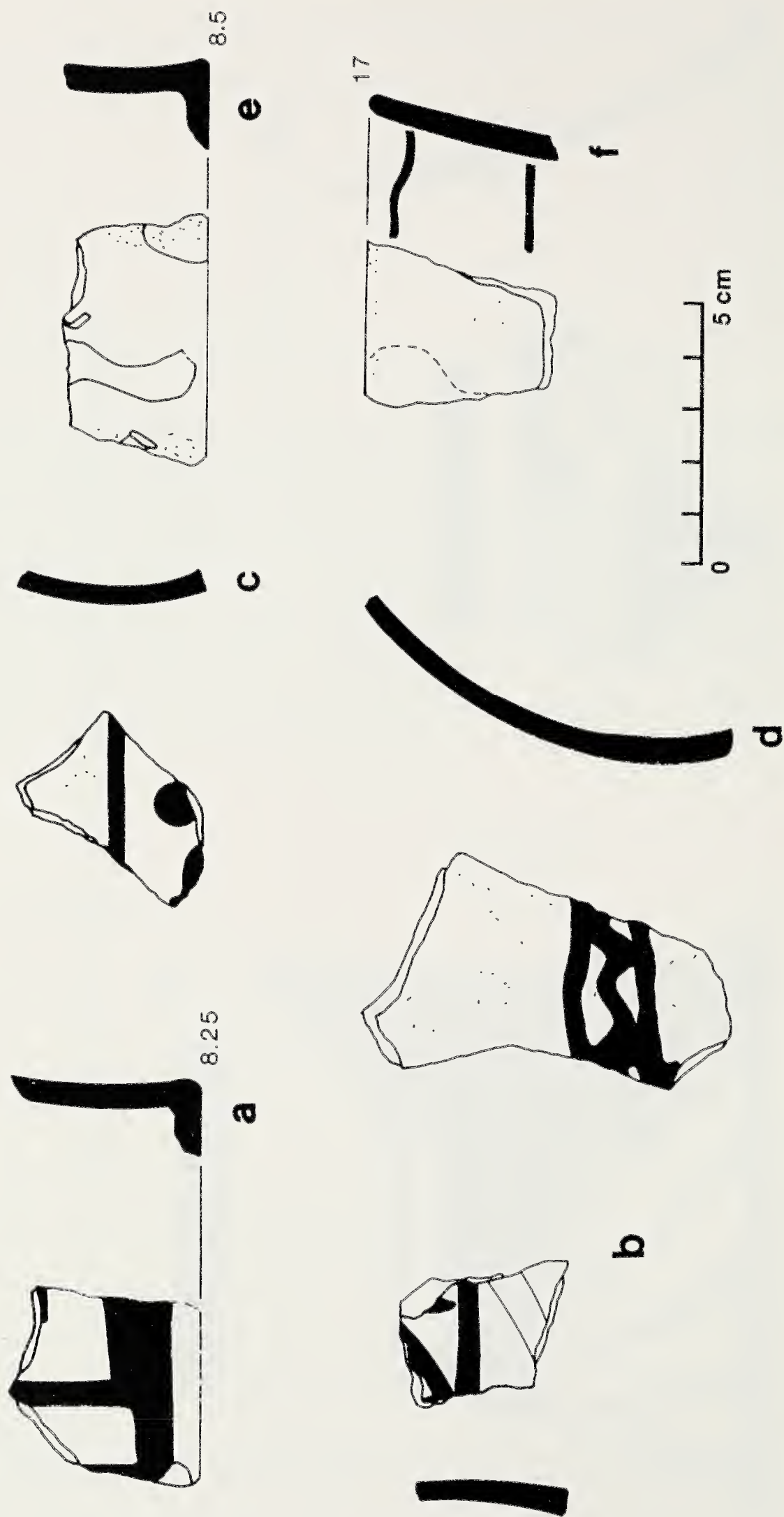


Fig. 14.—Tiwanaku-style pottery fragments recovered during surface collection at Jachakala. Number represents vessel rim or base diameter.

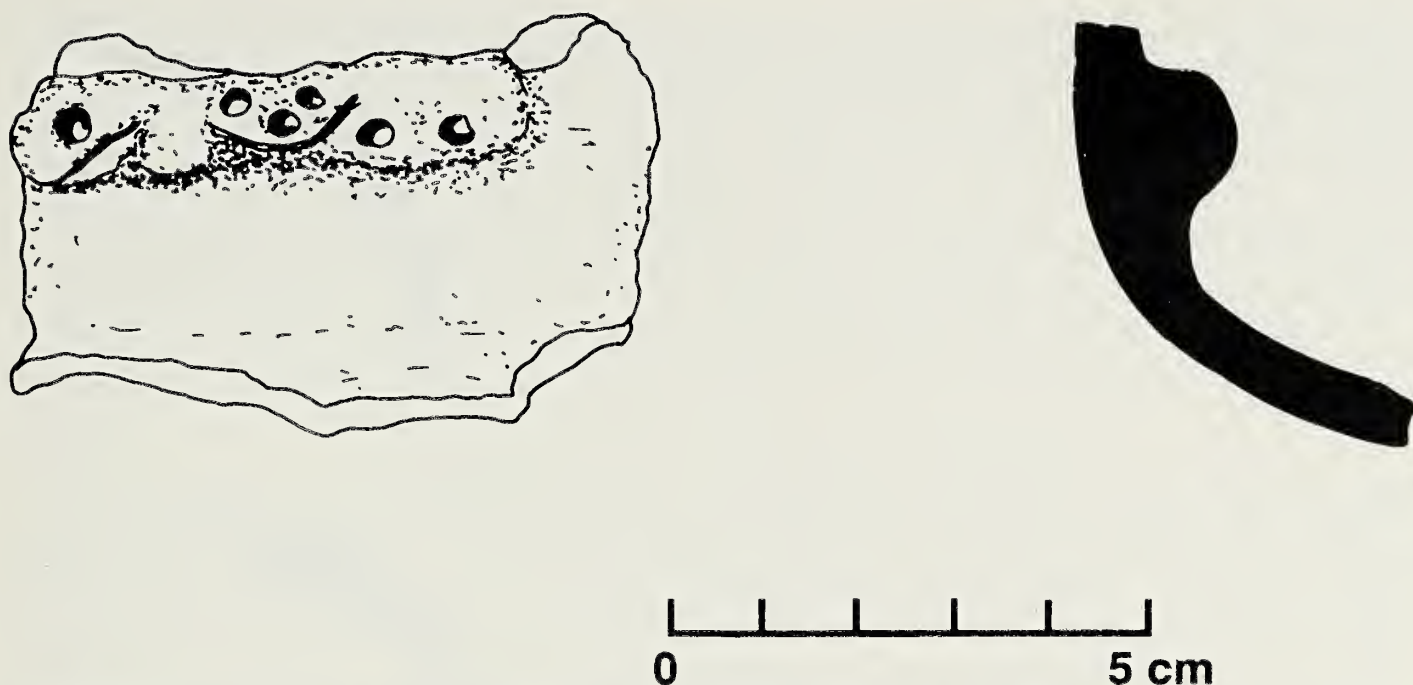


Fig. 15.—Fragment of Tiwanaku-style, punctate necklace *olla* from the surface of Jachakala.

Chile, and elsewhere in Bolivia were not found at Jachakala or other La Joya sites (Rydén, 1947, 1957; Wallace, 1957; Goldstein, 1985, 1989; Bermann, 1990). Thus, surface collection and excavation at Jachakala suggest that the site displays a limited assemblage of Tiwanaku-style pottery quite different from that found at other “Tiwanaku sites” such as Lukurmata, Omo, Khonko Wankani, and Condorchinoka (Rydén, 1947, 1957; Goldstein, 1985, 1989; Bermann, 1990).

Summary

On the basis of the stratigraphy of units 1 and 2, and the diachronic changes in defined ceramic types, we can divide the occupation at Jachakala into two phases: the Niñalupita Phase, corresponding roughly to the Upper Formative (A.D. 600–A.D. 800), and the Tiwanaku V-contemporary, Jachakala Phase (roughly A.D. 800–A.D. 1000). The beginning of the Jachakala Phase is marked by the presence of Tiwanaku-style pottery, a marked decrease in the use of mica temper, and a decline in the use of the Niñalupita Yellow and Intiraymi Mica types. Unfortunately, absolute dates from Jachakala are not yet available for these phases.

COMPARISON WITH TIWANAKU POTTERY

There is currently no comprehensive classification of Tiwanaku pottery. The works of Bennett (1934, 1936), Rydén (1947, 1957, 1959), Ponce (1970, 1981), and Wallace (1957), based on material from the Tiwanaku core area, remain the most valuable treatments of Tiwanaku iconography and ceramic styles. On the basis of stylistic divisions in decorated pottery, Bennett (1934) divided Tiwanaku prehistory into three phases: Early, Classic, and Decadent. Bennett’s sequence formed the basis for subsequent chronologies, although his phases have been renamed. The most widely used Tiwanaku sequence of five numbered periods (Tiwanaku I–V) was proposed by Ponce in 1961 (Disselhoff, 1968) and is based on both stylistic seriation and stratigraphy. The dating of each period is based on a series of radiocarbon dates (Ponce, 1981). More recently, investigators of Tiwanaku-style pottery at non-*altiplano* sites have been concerned with identifying a Tiwanaku “export” assemblage, and determining whether the Tiwanaku-style pottery was made locally or imported from the highlands (Goldstein, 1989).

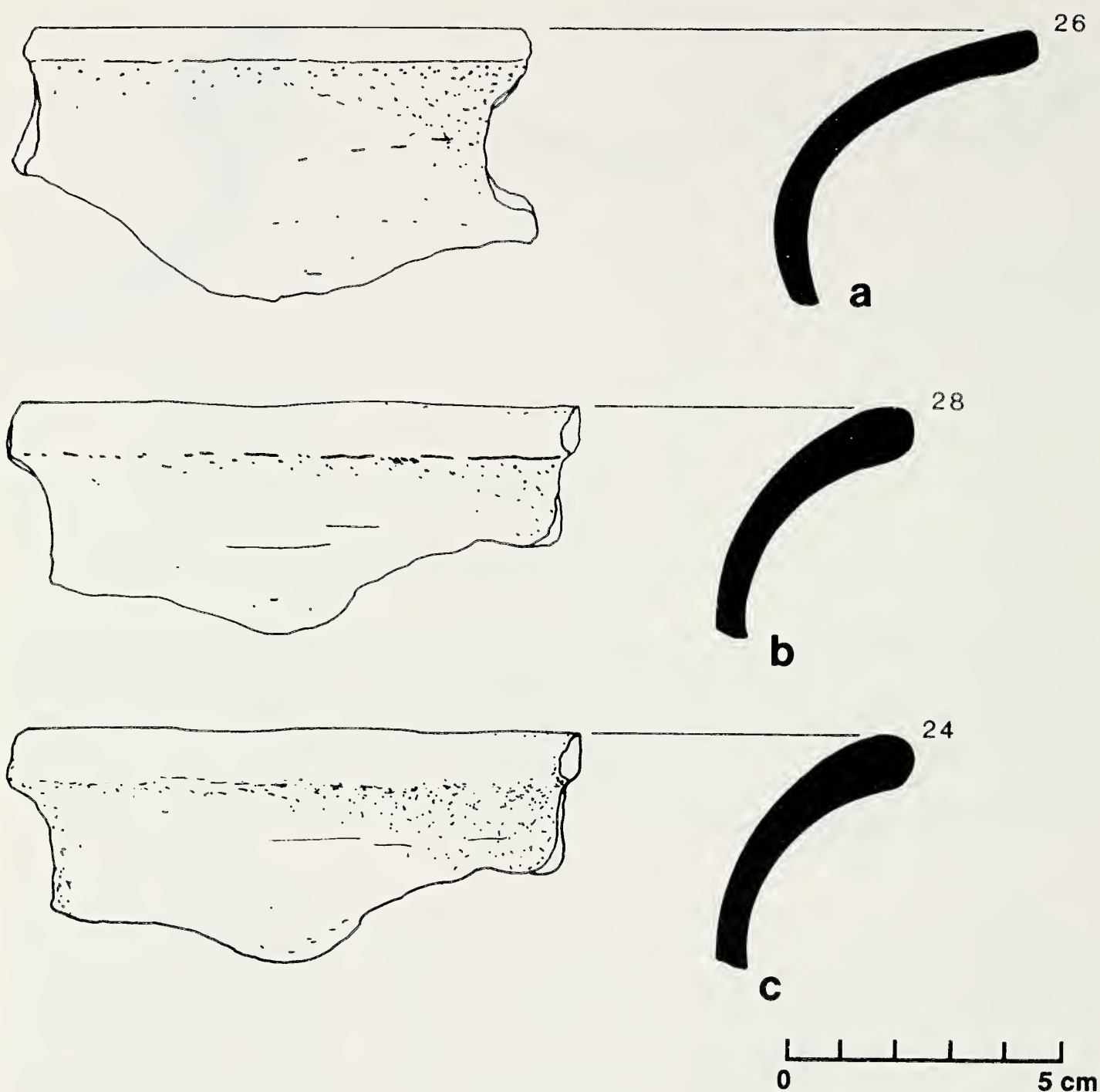


Fig. 16.—Typical Wankarani rim forms. These fragments are from the surface of the site of the Belén.

All of the Tiwanaku-style sherds at Jachakala represent typical Tiwanaku forms. The *kero* and flaring-side bowl (*tazone*) are common at Tiwanaku V Period sites throughout the Andes. The punctate necklace vessel is also an extremely common and widespread Tiwanaku plainware form, found at highland Tiwanaku sites, and non-*altiplano* sites in Cochabamba, Bolivia, and Moquegua, Peru (Rydén, 1947; Goldstein, 1985; Bermann, 1990).

Most of the decorated Tiwanaku-style ceramics at Jachakala resemble late Tiwanaku V Period pottery in slip color (orange), surface treatment (burnished slips), decorative technique (painting on a slightly wet slip), and decorative designs. Designs on Jachakala sherds include geometric patterns with wavy lines, and zoomorphic motifs (eagles and fish). Pendent loops occur on the interior rims of some Jachakala rim sherds, a late Tiwanaku V Period trait.

Ironically, the largest Tiwanaku-style specimen found at Jachakala is the only one that does not completely resemble pottery known from Tiwanaku. The entire,

intact *kero* was found just protruding from the ground during a casual walk over the site. While the form and color of this piece is entirely consistent with Tiwanaku pottery, the horizontal wavy line design is not found on pottery at Tiwanaku itself. The Jachakala *kero* may thus represent a new Tiwanaku V Period design or a vessel made locally in the "Tiwanaku-style."

Tiwanaku-style sherds from Jachakala were compared with specimens from Tiwanaku using the naked eye and a low power microscope. This comparison revealed no significant differences in paste or temper, suggesting that the Tiwanaku-style vessels at Jachakala were imports.

COMPARISONS WITH WANKARANI POTTERY

The only attempt at classification of Wankarani pottery is Ponce's (1970:32) preliminary division of Wankarani pottery into five categories based on surface treatment: (1) *pulido a espátula*, (2) *alisado liso*, (3) *pulido liso*, (4) *alisado a espátula*, (5) *misceláneos*. He (1970:32) uses this typology and secondary shape features to distinguish three Wankarani periods (Lower, Middle, and Upper), but the validity of this scheme has yet to be tested.

During surface collection at Wankarani sites in Oruro, we found many fragments of a previously undescribed Wankarani pottery type—Wilaque Black (Fig. 10), a roughly burnished ware fired in a reducing atmosphere. The examples illustrated were found on the surface of the Wankarani site of Wilaque, a site which also has small amounts of Tiwanaku-style pottery on the surface. The description of this new type is given in Appendix I.

The ceramics from Jachakala units 1 and 2 do not resemble in paste or surface treatment any of the known Wankarani pottery. Wankarani pastes range in color from orange-brown to dark gray, and are usually medium- to large-grained and slightly porous. The temper of Wankarani pottery in the La Joya area (mica, sand, and various minerals) tended to be larger (0.5–2.00 mm) than that of Jachakala sherds. It is more difficult to compare shapes, but one of the most common Wankarani forms, a bowl with a widely flaring rim, was not represented at Jachakala. Nor was the thickened or bulbous rim common to Wankarani vessels (Fig. 16b, c) seen on Jachakala specimens. No Jachakala pottery exhibited the basketry marks frequently seen on the base of Wankarani vessels. In brief, no Wankarani-style pottery (as currently defined) was recovered from the Jachakala excavations or the Jachakala surface collection.

CONCLUSIONS

Jachakala differs from Wankarani sites in: (1) site form, (2) associated pottery, and (3) domestic architecture. Jachakala is not a mound, and at least some of the architecture on the surface represents rectangular structures. Jachakala is also considerably larger than the Wankarani sites in the La Joya area. Traditionally in Andean archaeology, such differences would be sufficient to identify Jachakala as a distinct "archaeological culture." However, there are also some similarities to neighboring Wankarani sites that may represent local continuities. These similarities include the topographic setting (at the base of a *cerro*), circular dwellings, and the presence of large quantities of black basalt axes and slag from copper smelting.

Identifying a Tiwanaku-contemporary occupation in the Oruro region is merely the first step in exploring cultural evolution in this critical region in Bolivian prehistory. Much investigation remains to be done before we can study the pro-

cesses that led to the abandonment of the Wankarani sites, the founding of Jachakala, and whether interaction with Tiwanaku played a role in this process. Questions to be addressed with further research include: Was the Niñalupita occupation at Jachakala contemporaneous with occupations at nearby Wankarani sites? If not, how much time separates the abandonment of the Wankarani sites and the founding of Jachakala? Did subsistence and productive activities change between the Niñalupita and Jachakala phases?

Further research will be needed to assess the nature of interaction between the Tiwanaku polity and the Jachakala Phase population at Jachakala. Did some Jachakala households have greater access to Tiwanaku-style items than other households? Were the finished basalt axes at Jachakala items in a system of long-distance exchange with the Tiwanaku polity? Answering these questions will help us determine whether Jachakala represents a distinct post-Wankarani culture spread throughout the Oruro region, a small local center at the head of a Wankarani settlement hierarchy, or the "intrusive" residence of nonlocal colonists.

ACKNOWLEDGMENTS

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APPENDIX I

CERAMIC DESCRIPTIONS

This section presents a description of trial ceramic types defined on the basis of materials from both regional survey and the test excavations described above. A type-variety classification scheme was adopted for the initial ceramic analysis, even though the type-variety system has not traditionally been widely used in Bolivia. In general, we have followed the conventions set by Wheat et al. (1958), defining types in terms of gross characteristics of surface finish, paste, and decoration (Sinopoli, 1991:52; Steponaitis, 1983:50). Thus, varieties of the same type should share basic surface treatment and paste characteristics, but differ slightly from one another in technological attributes or design elements. The small size of the sherd sample from Jachakala did not allow definition of many varieties. A type and its component varieties are referred to as a “type cluster.” Since we were not able to distinguish component varieties for the pottery described below, it should be understood that these categories implicitly represent type clusters. Further subdividing into varieties will require larger samples than are currently available.

Our goal in the preliminary ceramic analysis was to classify specimens on the basis of characteristics seen in the smallest of nondiagnostic pottery fragments. As a result, the descriptions presented below generally reflect gross features of surface finish, paste, and temper observable to the naked eye, rather than technological attributes or vessel shape.

All but two of the types described below are “new” pottery types, based on the 1884 sherds excavated at Jachakala. The exceptions are Tiwanaku V Polychrome and Wilaque Black. The former is well-known and widely distributed, while the

latter, not represented at Jachakala, was recovered from Wankarani sites during surface survey.

Jachakala Brown and Jachakala Orange
(638 fragments)

These two poorly defined type clusters differed largely in paste color. There is a considerable range of variation in paste, temper, and finish characteristics within each type cluster. Most of the specimens in these type clusters have the following characteristics:

Paste and Temper.—Paste color is orange-brown, fully-fired, medium-grained, and slightly porous to well-knit. Temper consists of 0.3–1.2 fragments of old mica.

Surface Treatment.—Exterior color ranges from light brown to orange (5YR 5/4). Exteriors are unslipped, and roughly smoothed or smoothed. Interiors are similar.

Decoration.—None.

Form.—Forms include *ollas*, or slightly restricted bowls with flaring necks, straight-sided, flaring walled bowls, and shouldered jars with short necks.

Huitu Pampa Yellow
(382 fragments)

This is the type cluster counterpart grouping to the Jachakala Orange and Brown wares. In most instances, low sample sizes prevented defining true types within this subgrouping. Most of the specimens in this type cluster have the following characteristics:

Paste and Temper.—Paste color is yellow-brown (7.5YR 6/4) to yellow-orange (5YR 7/6). The pastes are generally medium-grained, fully-fired and slightly porous to well-knit. Tempering material ranges from sand, to crushed sherd, to gray, white, or black mineral grit.

Surface Treatment.—Exteriors are yellow-brown to yellow-orange, unslipped, and range from wiped to smoothed. Interiors are similar, and often display horizontal wiping marks.

Forms.—Same as the Mica wares.

Tiwanaku V Polychrome
(56 specimens from Jachakala surface, 22 from excavations)

Paste and Temper.—Paste color is orange (2.5YR 6/6) with light gray or brown core. Paste grains are fine to medium, and the paste is well-knit to slightly porous. Temper is not visible in many specimens, in others it consists of 0.3–1.0 mm gold mica.

Surface Treatment.—Vessel exteriors display an orange (2.5YR 5/6) or red (10R 5/4) burnished slip. Interiors are either slipped in the same color, or the color of the smoothed paste.

Decoration.—Painted decoration is in black (10YR 3/1), white (10YR 7/1), and orange (2.5YR 6/6).

Forms.—The two forms represented at Jachakala are *keros* and flaring-sided bowls (*tazones*). Other forms known from Tiwanaku include jars, pitchers, *incensarios*, and various bowls.

Distribution.—Tiwanaku V-style materials have a wide distribution throughout much of the south-central Andes, including the northern Lake Titicaca basin, the coasts of Chile and Peru, the southern Peruvian highlands, and Cochabamba,

Bolivia. Tiwanaku V-style ceramics have not been reported south of Lake Uru-Uru, making Jachakala, along with Toluma and Sokotina, the southernmost sites from which Tiwanaku pottery has been reported from domestic contexts.

La Joya Orange
(61 fragments)

Paste and Temper.—Paste color is very light orange-brown (7.5YR 7/4). The paste is fully-fired, medium-grained, and well-knit. Temper consists of 1.0–5.0 mm fragments of a soft red mineral, and 0.5–2.00 fragments of gold mica.

Surface Treatment.—Exteriors are unslipped, smoothed, and very light brown (7.5YR 7/4) in color. Interiors are unmodified paste.

Decoration.—None.

Forms.—Unknown, but probably restricted jars.

Titina Conglomerate
(31 specimens)

Paste and Temper.—The paste is orange (2.5YR 5/4) to orange-brown, fully-fired, coarse-grained, and slightly porous. The distinctive temper consists of 0.5–3.5 mm crushed red, yellow, and white material (crushed sherd?).

Surface Treatment.—Most exteriors are orange (2.5YR 5/4) and unslipped, displaying horizontal wiping marks. Roughly 10% of the fragments have a well-smoothed, orange wash on the exterior. Interior surfaces are similar.

Decoration.—None.

Forms.—Since most of the fragments recovered are body sherds, forms cannot be reconstructed. Rims are slightly flaring, with an exterior lip.

Intiraymi Mica
(82 fragments, all from LJ-2 excavations)

Paste and Temper.—The paste is dark red-brown (5YR 4/3), fully-fired, fine-grained, and well-knit. The most distinctive element of this type is the temper—0.3–1.0 mm gold mica—that makes up roughly 20% of the paste.

Surface Treatment.—Exteriors are dark red-brown to dark gray (5YR 4/1), well-smoothed to slightly burnished. Interiors have a similar color, but are generally smoothed rather than burnished.

Forms.—Forms cannot be reconstructed, but rim fragments suggest a vertically-sided, straight-walled vessel with a simple, direct rim. Rim diameters range from 23–29 cm.

Decoration.—None.

Niñalupita Yellow
(73 fragments, all from LJ-2 excavations)

Paste and Temper.—Paste color ranges from light brown (7.5YR 7/4) to pinkish-orange (5YR 6/4). Paste is fully-fired, medium- to coarse-grained, and well-knit. Tempering material varies considerably, but always includes 0.4–2.5 mm gold mica (muscovite?) and often small fragments of a crushed white mineral.

Surface Treatment.—Vessel exteriors have a roughly smoothed yellowish-green (5Y 8/3) slip. Vessel interiors, lacking a slip, are the same color as the paste, and roughly smoothed to wiped.

Decoration.—None.

Form.—Complete vessel forms could not be reconstructed. Rim sherds suggest

two distinct forms: (a) an open, straight-walled bowl (rim diameter of 15–20 cm); and (b) an open or slightly constricted flaring-rim *olla* (rim diameter 35–39 cm). The latter form has a direct base with a diameter of 15–17 cm.

Wilaque Black

Paste and Temper.—Paste color is light gray (2.5YR 5/0) and fully-fired, indicating firing in a reducing atmosphere. The paste is medium-grained and slightly porous. Temper consists of 0.5–2.0 mm crushed gray grit.

Surface Treatment.—Vessel exteriors vary from deep gray to black (7.5YR 3/0) and are smoothed or roughly burnished rather than slipped. The interior surfaces of open vessels resemble the exteriors. The interior surfaces of constricted vessels consist of unmodified paste.

Decoration.—None.

Forms.—Only one complete form is known. This is displayed in the Oruro Museum. It is a fluted beaker with a flat, wide disk base. Fragments from Wilaque suggest two other forms: a shoulder jar with a constricted neck, and an open or slightly restricted, flaring lip *olla*. Bases tend to be of the disk form, and basket marks are generally present on the bottom of the base.

Distribution.—This group represents a previously undescribed type of Wankarani ceramics. It was found at a number of Wankarani mound sites in the survey area, particularly Wilaque. Nonsystematic examination of surface remains at other Wankarani sites suggests that Wilaque Black does not occur at some Wankarani sites, occurs in small quantities at others (2–3% of the total surface ceramics), and is most common at Wilaque (15%).

APPENDIX II

DESCRIPTIONS OF ILLUSTRATED CERAMIC

Figure 8.—Exterior: Orange-brown (5YR 6/6); no slip; roughly smoothed with horizontal marks. Interior: Orange-brown (5YR 6/6); no slip; roughly smoothed. Paste: Orange with brown (7.5YR 6/2) core; fine-grained; medium-knit. Temper: 0.3–1.5 mm gold mica; sand; 8%.

Figure 9.—(a) Exterior: Very light yellow-brown (10YR 6/3) no slip; roughly smoothed. Interior: Same. Paste: Yellow-brown to orange; medium-grained; poorly-knit. Temper: 0.5–3.3 mm gold mica; 3%. (b) Exterior: Light pink-brown (5YR 7/4) slip or wash; smoothed. Interior: Missing. Paste: Orange (2.5YR 5/6); medium-grained; slightly porous. Temper: 0.5–2.8 mm white, red, orange mineral; crushed sherd?; 10%. (c) Exterior: Yellow-green (2.5Y 7/2) slip; smoothed. Interior: Orange (2.5YR 6/6) paint. Paste: Yellow-brown; fully-fired; coarse; very porous. Temper: 1.0–4.5 mm white, gray, black, red mineral; 8%. (d) Exterior: Brown (5YR 5/3) no slip; roughly smoothed with horizontal marks. Interior: Orange (2.5YR 6/6) slip; roughly smoothed. Paste: Brown; fully-fired; fine-grained; porous. Temper: 0.5–1.0 mm gold mica; 3%. (e) Exterior: Orange (2.5YR 5/4); no slip; wiped with horizontal marks. Interior: Orange (2.5YR 5/4); no slip; wiped with horizontal marks. Paste: Orange to orange-brown; fully-fired; coarse-grained; slightly porous. Temper: 0.5–3.5 mm red, white, yellow mineral (crushed sherd?); 10%. (f) Exterior: Light yellow-brown (10YR 8/4) slip; roughly smoothed. Interior: Light yellow-brown (10YR 8/4) slip; roughly smoothed. Paste: Dark gray; fully-fired; medium-grained; medium-knit. Temper: 1.0–2.0 mm mica(?).

Figure 10. —(a) Exterior: Gray-black (7.5YR 3/0); no slip; roughly burnished. Interior: Gray-black (7.5YR 3/0); no slip; unmodified. Paste: Light-gray (2.5Y 5/0); fully-fired; medium-grained; slightly porous. Temper: 0.5–2.0 mm crushed gray mineral; 5%. (b) Exterior: Gray-black (7.5YR 3/0); no slip; roughly smoothed. Interior: Gray-black (7.5YR 3/0); no slip; unmodified. Paste: Light-gray (2.5Y 5/0); fully-fired; medium-grained; slightly porous. Temper: 0.5–2.0 mm crushed gray mineral; 5%. (c) Exterior: Gray-black (7.5YR 3/0); no slip; roughly burnished. Interior: Gray-black (7.5YR 3/0); no slip; unmodified. Paste: Light-gray (2.5Y 5/0); fully-fired; medium-grained; slightly porous. Temper: 0.5–2.0 mm crushed gray mineral; 5%.

Figure 13. —(a) Exterior: Orange (5YR 6/6) burnished slip with black (5YR 3/2) painted decoration. Interior: Orange (5YR 6/6) burnished slip with black (5YR 3/2) painted decoration to 4.5 cm below rim. Below 4.5 cm, yellow-brown; (7.5YR 6/4); no slip; burnished. Paste: Orange with slight gray core; medium-grained; slightly porous. Temper: 0.5–2.0 mm white mineral; 3%. (b) Exterior: Dark red (10R 5/4) burnished slip with black (10YR 3/1), white (10YR 9/1), orange (2.5YR 6/6) painted decoration. Interior: Red slipped partway down. Below this orange (5YR 6/6) no slip; smoothed. Paste: Orange (5YR 6/6) with gray-brown core; medium-grained; well-knit. Temper: 0.3–1.0 mm gold mica; 3%.

Figure 14. —(a) Exterior: Red (10R 5/6) burnished slip with black (2.5YR 3/0) or orange (2.5YR 5/6) painted decoration. Interior: Orange; no slip; wiped. Paste: Orange with light orange-brown core; medium-grained, medium-knit. Temper: not visible. (b) Exterior: Orange (2.5YR 4/4) slightly burnished slip with red (10R 3/4) and black (7.5YR 3/0) painted decoration. Interior: Orange (2.5YR 4/4) slightly burnished slip with black (7.5YR 3/0) painted decoration. Paste: Orange (10R 5/8); fully-fired; medium-grained; well-knit. Temper: 0.8–1.4 mm crushed gray mineral; 8%. (c) Exterior: Orange (10R 5/8) burnished slip with black (2.5Y 2/0) painted decoration. Interior: Orange (10R 5/6); no slip; smoothed. Paste: Orange; fully-fired; medium-grained; well-knit. Temper: Not visible. (d) Exterior: Orange (2.5YR 5/4); no slip; smoothed to slightly burnished with vertical marks; black (5YR 3/1) painted decoration. Interior: Orange (2.5YR 5/4); no slip; smoothed with vertical marks. Paste: Orange; fully-fired; medium-grained; well-knit. Temper: 0.3–0.8 mm gold mica. (e) Exterior: Orange (2.5YR 6/6) burnished slip with black (7.5YR 3/0) painted decoration. Interior: Orange (5YR 7/8); no slip; smoothed. Paste: Yellow-orange with slight gray core; fine-grained; medium-knit. Temper: Not visible. (f) Exterior: Eroded red (10R 4/4) burnished slip with black painted decoration. Interior: Eroded red (10R 4/4) burnished slip with black (5YR 3/1) and white (5YR 7/2) painted decoration. Paste: Light brown; fully-fired; medium-grained; well-knit. Temper: Not visible.

Figure 15. —Exterior: Orange-brown (2.5YR 5/4); no slip; wiped. Interior: Brown (5YR 6/4); unmodified. Paste: Brown; fully-fired; medium-grained; well-knit. Temper: Sand(?); white, gray crushed quartz; 12%.

Figure 16. —(a) Exterior: Orange-brown; no slip; roughly smoothed with horizontal marks. Interior: Orange-brown; no slip; smoothed with vertical marks. Paste: Orange; fully-fired, medium-grained; medium-knit. Temper: 0.5–2.0 mm gold mica; white mineral; 3%. (b) Exterior: Brown-orange (2.5YR 6/6), no slip; roughly smoothed with horizontal marks. Interior: Same; wiped with horizontal marks. Paste: Brown-orange (2.5YR 6/6) with light gray (10R 6/1); medium-grained; medium-knit. Temper: 0.3–2.5 mm gold mica, black mineral; 0.5–1.0

mm white mineral; 5%. (c) Exterior: Red-orange (5YR 5/4); roughly smoothed, no slip; horizontal smoothing marks. Interior: same, but burned. Paste: Red-brown (5YR 5/4) with light gray (10R 5/1) core; medium-grained; medium-knit. Temper: 0.5–1.0 mm gold mica, black, white mineral; 3%.

NOTES ON *AMBLYSCHIRTES* SCUDDER, WITH THE
DESCRIPTION OF TWO NEW SUBSPECIES
(INSECTA: LEPIDOPTERA: HESPERIIDAE: HESPERIINAE)

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ABSTRACT

Some systematic and nomenclatural problems in *Amblyscirtes* (Lepidoptera: HesperIIDae: HesperIIDae) are resolved. *Amblyscirtes prenda* Evans, 1955, is returned to its original status, *A. tolteca prenda* Evans. *Amblyscirtes elissa arizonae* (Arizona, USA) and *A. fimbriata pallida* (Mexico) are described as a new subspecies. The upper and lower surfaces of *A. tolteca* Scudder, *A. tolteca prenda*, *A. elissa elissa* Godman, *A. elissa arizonae*, *A. fimbriata fimbriata* (Plötz), and *A. fimbriata pallida* are illustrated. A synonymic checklist of all *Amblyscirtes* is presented.

INTRODUCTION

When I reviewed *Amblyscirtes* (Freeman, 1973) I stated "there are 31 species in the genus *Amblyscirtes* and for the present I do not recognize any subspecies." Since then I have examined a number of specimens of *Amblyscirtes* from several museums and private collections. On the basis of this new material and with the work of Burns (1990) on the genitalia of the genus, I have changed my concept regarding the status of *Amblyscirtes prenda* and the arrangement of the various species. I now recognize 28 species and three subspecies in *Amblyscirtes* based on genitalic morphology, occurrence of a stigma or brands, and the basic spot arrangement. I follow Evans (1955) in making a distinction between stigma and brand or brands, which are found on the primaries of males in species of HesperIIDae. The term stigma applies to a specialized patch of tubular scales and androconia extending between and sometimes crossing the veins, whereas the term brand or brands applies to the same type of specialized patch or patches but which extends parallel with the vein or veins. I have followed the English system of numbering the veins of each wing from the lowest vein upward, and the space is immediately below the numbered vein. This system was used in describing most of the species of *Amblyscirtes*, and by Burns (1992) in describing a new species of *Halotus* Godman from Mexico. A discussion of the status of *Amblyscirtes prenda* Evans and the description of two new subspecies of *Amblyscirtes* follows.

Material was examined in the following collections: American Museum of Natural History, New York, New York (AMNH); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (CMNH); private collection of J. P. Brock, Tucson, Arizona (JPB); private collection of H. A. Freeman, Garland, Texas (HAF); United States National Museum of Natural History, Washington, D.C. (USNM).

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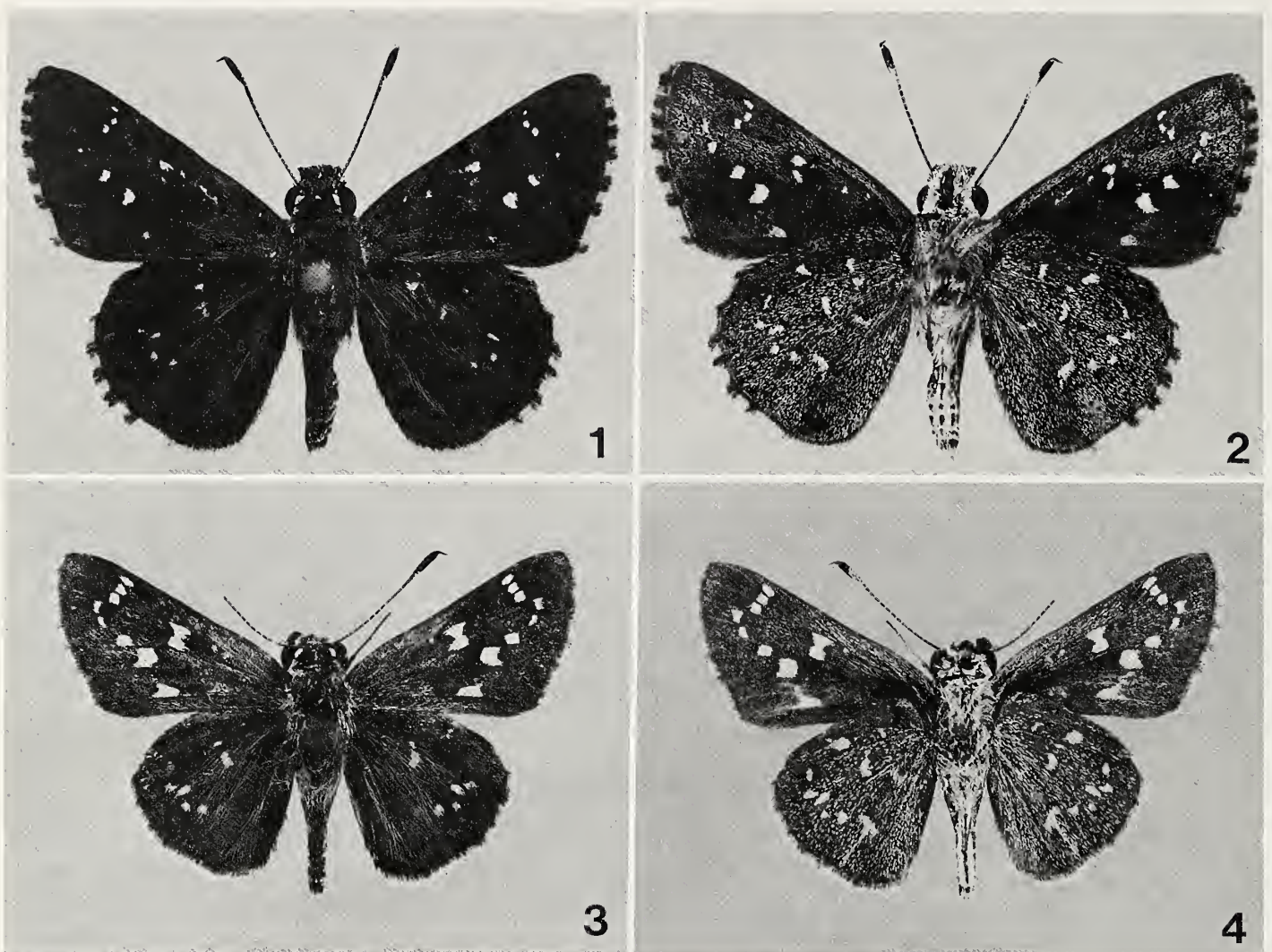


Fig. 1–4.—Subspecies of *Amblyscirtes tolteca* Scudder: 1, *A. t. tolteca* Scudder, male, upper surface, from Mexico, Puebla, Patla, 1800 ft, 16 June 1991 (John Kemner); 2, lower surface of specimen in Fig. 1; 3, *A. t. prenda* Evans, male, upper surface, from Mexico, Sonora, Tepoca, Route 16, 15 July 1988 (D. D. Mullins); 4, lower surface of specimen in Fig. 3.

SYSTEMATICS

Amblyscirtes tolteca tolteca Scudder (Fig. 1–2)

Amblyscirtes tolteca Scudder, 1872:55.

Type Locality.—MEXICO. *Oaxaca*: Tehuantepec.

Diagnosis.—As pointed out by Burns (1990) this species belongs in a group containing *Amblyscirtes celia* (Skinner, 1895) and *A. belli* Freeman, 1941, based on the male genitalia and general maculation. I, as well as Burns (1990), have examined the genitalia of all of the species in the genus *Amblyscirtes* and have found that the basic characteristics are the presence of a long, narrow aedeagus split distally into two, more or less parallel, linearly toothed ends; a long narrow saccus; and a tegumen with a delicate, middorsal caudally arching prong over a somewhat oval opening. Burns (1990) found that both *A. celia* and *A. belli* show striking asymmetry of the terminal end of the long aedeagus. He stated, “along the left side of the aedeagus just before its end, a large, thin triangular plate with a long base curves outward and upward forming a conspicuous pointed titillator (Fig. 2–3, 5–6).” He noted that this structure is also found in *A. tolteca*, but not in any other species of *Amblyscirtes*, and that the general maculation is similar in all three species, especially on the lower surfaces of the secondaries. *Amblyscirtes tolteca* has the greatest spot-pattern development, *A. celia* less well-developed,

and *A. belli* the least developed. On the upper surfaces of the secondaries in *A. tolteca* there are usually five small white spots, one in the cell and four discal, whereas in *A. celia* and *A. belli* these spots are absent. On the upper surface of each primary in males of *A. tolteca* there is a long brand adjacent to the cubitus, between the origins of veins 3 and 2, and a short one under vein 2. These brands are present in both *A. celia* and *A. belli* as well as in many other species, but are shorter.

Description.—See Fig. 1, 2.

Specimens Examined.—(22 males, 11 females). *Nayarit*: 5 mi SW Compostela, 2500 ft, 7 Aug. 1989, 3 males, 4 females (J. Kemner, HAF); Tepic, Sept. 1964, 1 female (T. Escalante, HAF). *Tamaulipas*: Ciudad Victoria, June 1966, 1 male (H. A. Freeman, AMNH); Mante, June 1967, 2 males (H. A. Freeman, AMNH); El Salto, 24 Aug. 1967, 1 male (H. L. King, AMNH); Gomez Farias, 14 July 1973, 1 male (W. W. McGuire, AMNH). *San Luis Potosi*: 6 mi S Ciudad Valles, Hotel Covadonga, June 1966, 4 males, 2 females (H. A. Freeman, AMNH); Tamazunchale, July 1963, 1 male (H. A. Freeman, AMNH), 24 Aug. 1967, 1 male (H. L. King, AMNH); La Mera Ceiba, 31 July 1987, 1 female (J. Kemner, HAF). *Puebla*: Patla, 1800 ft, 16 June 1991, 1 male (J. Kemner, CMNH). *Guerrero*: Acapulco, June 1936, 1 male (H. A. Freeman, AMNH). *Oaxaca*: Candelaria, 1800 ft, 26 June 1988, 1 male (J. Kemner, HAF); Pluma Hidalgo, 4000 ft, 17 Aug. 1988, 1 male (J. Kemner, HAF); Zipolite sea level, 10 Aug. 1990, 1 female (J. Kemner, HAF). *Chiapas*: El Aguacero, 2500 ft, 27 July 1988, 1 male (J. Kemner, HAF), 13 July 1991, 3 males (J. Kemner, HAF).

Discussion.—*Amblyscirtes tolteca tolteca* is found over most of Mexico, the exceptions being the Sonoran desert and Baja California. Specimens that I have observed and collected were most often associated with jungle environments, feeding on flowers or “puddling” at moist spots or near rivers. At times *A. t. tolteca* was abundant near the Río Valles, 6 mi S Ciudad Valles, Hotel Covadonga, S.L.P.

Amblyscirtes tolteca prenda Evans, revised status
(Fig. 3–4)

Amblyscirtes tolteca prenda Evans, 1955:389.

Amblyscirtes prenda: Freeman, 1973:50.

Type Locality.—UNITED STATES. *Arizona*.

Diagnosis.—This subspecies differs from *A. t. tolteca* in being slightly smaller: males average total expanse 25 mm ($n = 10$), females average 26 mm ($n = 1$), whereas *A. tolteca tolteca* males average 27 ($n = 22$), females 29 mm ($n = 11$). *Amblyscirtes tolteca prenda* is paler in coloration, especially on the under surface, due to a heavy concentration of violet-gray scales along the costa and apex of the primaries and on all of the secondaries, whereas *A. tolteca tolteca* appears darker brownish-black due to the absence of the violet-gray scales. The spots are more sharply defined in *A. tolteca prenda* than in *A. t. tolteca*.

The genitalia and the brands are the same in both.

Description.—See Fig. 3–4.

Specimens Examined.—(10 males, 1 female). UNITED STATES. *Arizona*: Tucson, 22 June 1955, 1 male (Lucian Harris, Jr., HAF). MEXICO. *Sonora*: 10 mi NW Alamos, 13 Aug. 1970, 1970, 1 male (B. Patterson, HAF); Tepoca, Rt. 16, 5 July 1988, 1 male (D. D. Mullins, CMNH). *Baja California Sur*: Ayo. Candelaria, 26 Nov. 1961, 1 male; Ro. Palmarito, 5 Nov. 1961, 1 male, 27 Oct. 1961, 1 male, 21 Oct. 1961, 1 male; Guaycura Hotel grounds, La Paz, 19 Oct. 1961, 1 male, 21 Oct. 1961, 1 male; Puerto Chileno, 22 Nov. 1961, 1 male; Cabo San Lucas, 23 Nov. 1961, 1 female (all CMNH; Cary-Carnegie Expedition 1961, C. M. Acc. 20082).

Discussion.—*Amblyscirtes tolteca prenda* seems to be confined to desert environments as the only specimens that I have seen were collected in Arizona, the Sonoran Desert and Baja California.

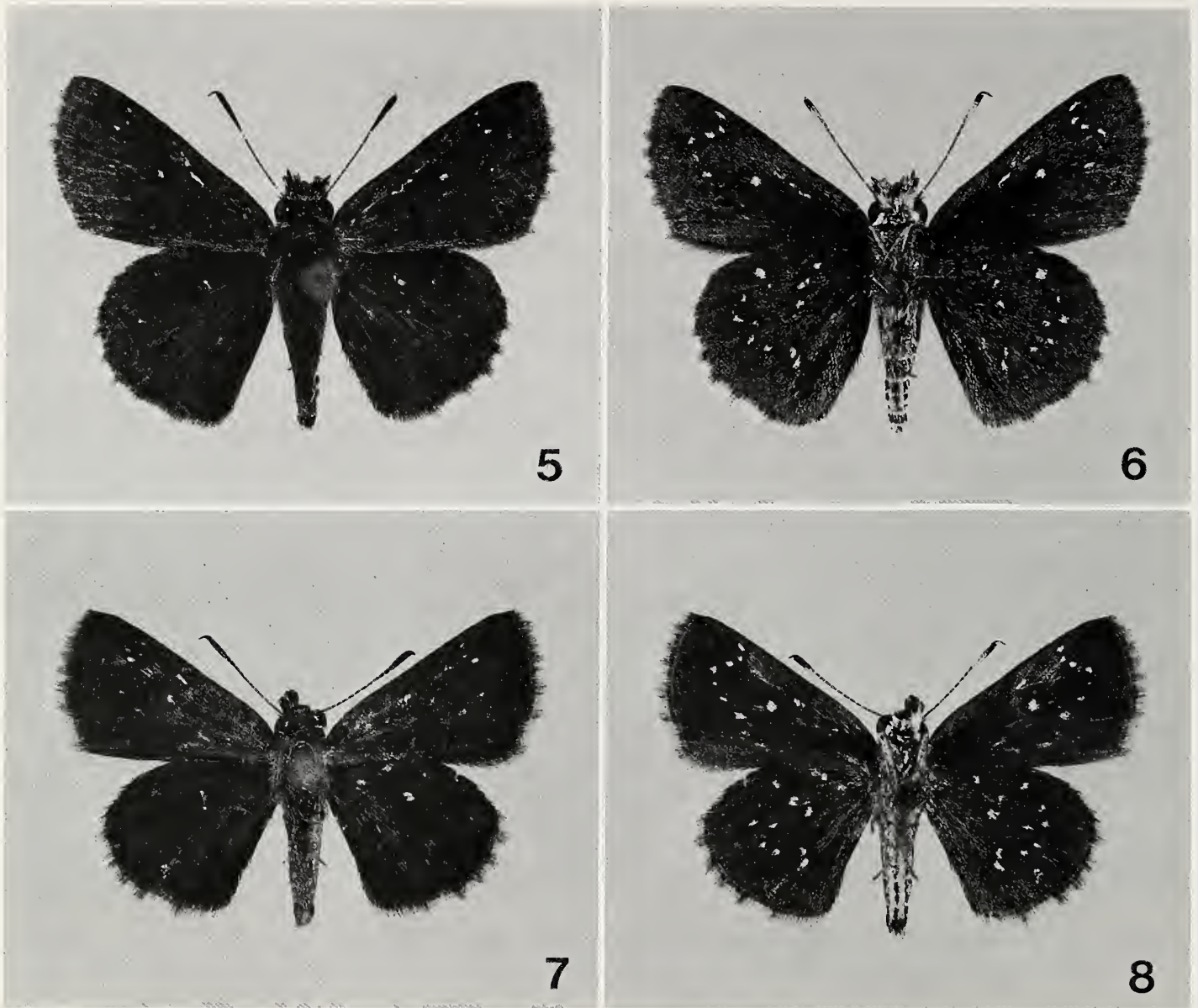


Fig. 5–8.—*Amblyscirtes elissa elissa* Godman: 5, male upper surface, from Mexico, Oaxaca, road to Grutas de San Sebastian, 5500 ft, 13 August 1991 (John Kemner); 6, lower surface of specimen in Fig. 5; 7, female, upper surface, from Mexico, Oaxaca, road to Grutas de San Sebastian, 5500 ft, 13 August 1991 (John Kemner); 8, lower surface of specimen in Fig. 7.

Amblyscirtes elissa elissa Godman
(Fig. 5–8)

Amblyscirtes elissa Godman, (1900): In Godman and Salvin, 1887–1901:505, plate 95, fig. 40–41.

Type locality.—MEXICO. Guerrero.

Diagnosis.—On the upper surface *A. e. elissa* is very similar to *Amblyscirtes alternata* (Grote and Robinson, 1867) in being dark grayish-brown with the three apical spots being needle points and in having a minute, indistinct, whitish discal spot in space 3. However most males of *A. e. elissa* have no spots. *Amblyscirtes alternata* has the brand reduced to a tiny dash above vein 2 against the cubitus, whereas *A. e. elissa* has a long, thin gray stigma. The lower surface of the wings of *A. e. elissa* slightly resemble *Amblyscirtes eos* (W. H. Edwards, 1871), in that the white spots are sharply defined on the secondaries. On the upper surface in *A. e. elissa* the fringe of both wings is plain brown in the males, with very fresh specimens having a slight indication of being checkered, whereas both *eos* and *alternata* have their fringes distinctly checkered in both sexes. Average total expanse of males 22 mm ($n = 26$), females 23 mm ($n = 2$).

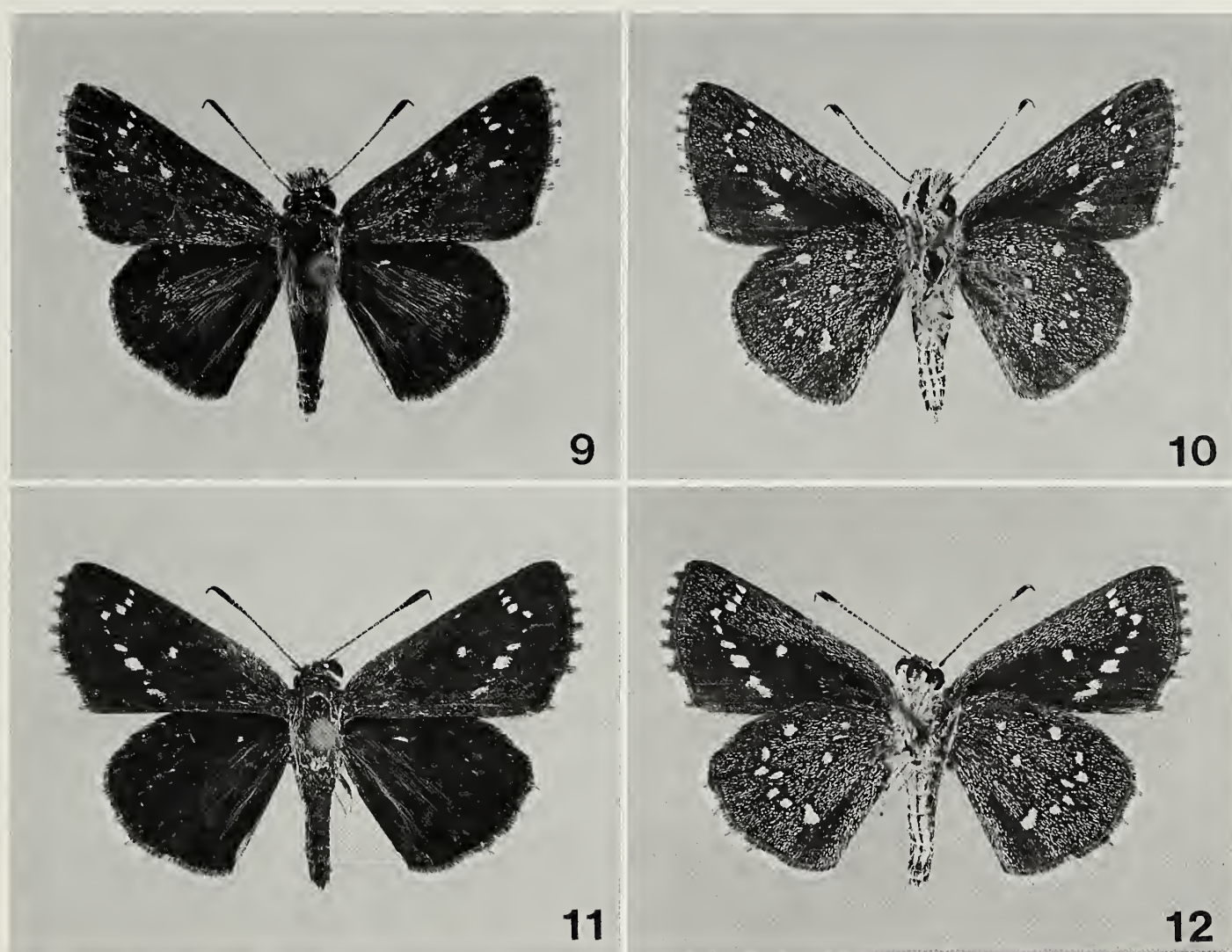


Fig. 9–12. — *Amblyscirtes elissa arizonae* Freeman: 9, male holotype, upper surface, from USA, Arizona, Santa Cruz Co., 0.5 mile W Kino Springs, 20 July 1986 (Jim P. Brock); 10, lower surface of specimen in Fig. 9; 11, female paratype, upper surface, from USA, Arizona, Santa Cruz Co., 0.5 mile W Kino Springs, 23 July 1989 (Jim P. Brock); 12, lower surface of specimen in Fig. 11.

Specimens Examined. — (26 males, 2 females). MEXICO. *Guerrero*: Acahuizotla, Hwy. 95, 3000 ft, 11 Aug. 1989, 1 male (J. Kemner, HAF), July 1960, 1 male (T. Escalante, AMNH); Iguala, Aug. 1951, 1 male (T. Escalante, AMNH). *Oaxaca*: Hwy. 175, 5 mi N city of Oaxaca, 6000 ft, 13 Aug. 1989, 1 male (J. Kemner, HAF), 30 Aug. 1989, 2 males (J. Kemner, HAF); road to Grutas de San Sebastian, 5500 ft, 13 Aug. 1991, 5 males, 1 female (J. Kemner, HAF), 1 male, 1 female (J. Kemner, CMNH). *Chiapas*: El Aguacero, 2500 ft, 3 Sept. 1989, 6 males (J. Kemner, HAF), 8 Sept. 1989, 7 males (J. Kemner, HAF), 13 July 1991, 1 male (J. Kemner, HAF).

Discussion. — From the specimens that I have examined, *A. e. elissa* seems to be confined to the state of Guerrero, Oaxaca, and Chiapas, Mexico. This was a rare species in collections until John Kemner collected a number of specimens in Oaxaca and Chiapas.

Amblyscirtes elissa arizonae Freeman, **new subspecies**
(Fig. 9–12)

Type Locality. — UNITED STATES. *Arizona*: Santa Cruz Co., 0.5 mi W Kino Springs.

Diagnosis. — This subspecies differs from *A. e. elissa* in a number of ways. Males have well-developed white spots on the upper and under surfaces of the primaries, three subapical in spaces 6, 7, 8, one in the cell, one in space 3, and sometimes

faint ones in spaces 2, 4, and 5, whereas *A. elissa elissa* does not have any of these spots well-defined, with only faint subapical and a discal spot in space 3 sometimes present. The fringe on the primaries of *A. elissa arizonae* is usually distinctly checkered, whereas in *A. elissa elissa* it is usually plain brown. On the under surfaces of the primaries in *A. elissa elissa*, the only white spots present are faint ones in the cell and in spaces 3, 4, 5, 6, 7, and 8, all of which may be absent. In *A. elissa arizonae* the white spots are usually well-developed and extend from space 1 to space 8, with a distinct spot in the cell. The under surfaces of the secondaries have the white spots better defined in *A. elissa arizonae*, especially the one in the cell. The females of *A. elissa arizonae* have all spots better defined than in males with some specimens having spots in spaces 1a and 1b on the upper and lower surfaces of the primaries. *Amblyscirtes elissa arizonae* is slightly larger than *A. elissa elissa*, as the average total expanse of the males is 24 mm ($n = 34$), females 25 mm ($n = 22$). The genitalia and the stigma are the same in both subspecies.

Specimens Examined.—(34 males, 22 females). UNITED STATES. *Arizona*: Santa Cruz Co., 0.5 mi W Kino Springs, 20 July 1986, 3 males, 4 females (J. P. Brock, HAF), 1 male (J. P. Brock, CMNH), 23 July 1989, 1 female (J. P. Brock, CMNH); St. Hwy. 82, 0.5 mi SW Kino Springs, 21 July 1991, 1 male, 1 female (J. P. Brock, JPB); 8 males, 4 females (J. P. Brock, HAF), 23 July 1989, 1 male, 3 females (J. P. Brock, JPB); Sycamore Canyon, near Ruby, 25 July 1990, 2 males (J. P. Brock, JPB), 2 males (J. P. Brock, HAF), Peña Blanca Lake, 19 July 1990, 2 males, 1 female (J. P. Brock, HAF), 1 male, 1 female, reared on *Bouteloua curtipendula* (Poaceae) (J. P. Brock, JPB), 2 Aug. 1989, 1 male, 6 females (D. D. Mullins, HAF). MEXICO. *Sonora*: creek at 5000 ft, Trinidad-Yecora rd., 6 mi W Yecora, 31 July 1984, 2 males (J. P. Brock, JPB), 3 males (J. P. Brock, HAF); Trinidad-Yecora rd., 5 mi NW of Yecora, 21 July 1985, 2 males, 1 female (J. P. Brock, JPB); Nacori Chico-Tres Ríos rd., Jct. of El Rito, 15–16 July 1988, 1 male (J. P. Brock, JPB), 2 males (J. P. Brock, HAF); 13 mi E of El Novillo, 12 Aug. 1985, 1 male (J. P. Brock, JPB). *Jalisco*: Chapala, 19 June 1978, 1 male (P. M. Jump, HAF).

Type Material.—Holotype: male, *Amblyscirtes elissa arizonae* Freeman; Arizona: Santa Cruz Co., 0.5 mi W Kino Springs, 20 July 1986, Jim P. Brock; length of fore wing 12.2 mm, length of hind wing 9.1 mm; deposited in CMNH. All of the specimens listed under Specimens Examined are paratypes and will be placed in the following museums and private collections: CMNH, USNM, AMNH, Allyn Museum of Entomology, Sarasota, Florida (AME), JPB, D. D. Mullins (DDM), and HAF.

Discussion.—This subspecies occurs from southern Arizona to Jalisco, Mexico. It differs from *A. elissa elissa* by having the maculation much better developed and by being slightly larger in total expanse.

Amblyscirtes fimbriata fimbriata (Plötz)
(Fig. 13–16)

Hesperia fimbriata Plötz, 1882:322.

Pamphila bellus W. H. Edwards, 1884:57.

Type Locality.—MEXICO.

Diagnosis.—The most similar species is *Amblyscirtes phylace* (W. H. Edwards, 1878) based on maculation and the presence of a stigma in the males. *Amblyscirtes f. fimbriata* is uniform dark brownish-black with no spots, the fringe in both sexes is orange on both wings, the head and palpi are orange in both sexes, and males have a long, narrow, broken gray stigma extending from the origin of vein 3 to vein 1. *Amblyscirtes phylace* is uniform dark grayish-black with no spots. In males the fringe of both wings is white and in females sordid white to light gray. In

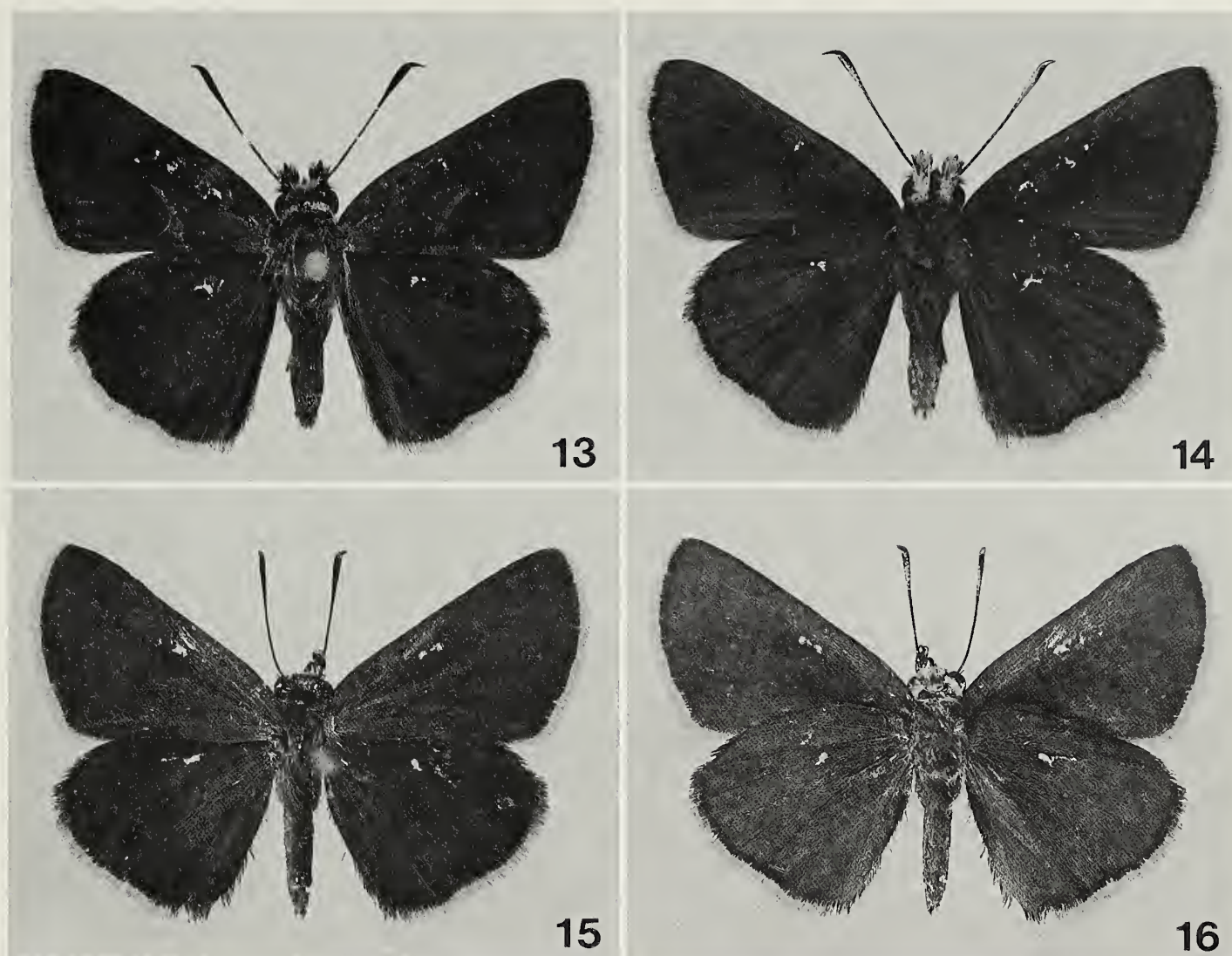


Fig. 13–16.—*Amblyscirtes fimbriata fimbriata* (Plötz): 13, male, upper surface, from Mexico, Oaxaca, Sierra Juarez, La Cumbre-El Punto, 9500 ft, 13 April 1989 (John Kemner); 14, lower surface of specimen in Fig. 13; 15, female, upper surface, from USA, Arizona, Cochise Co., Pinery Canyon, 6500 ft, 11 July 1960 (H. A. Freeman); 16, lower surface of specimen in Fig. 15.

males the head and palpi are light orange and in females yellowish-white. In males the stigma is short and broad, and extends from the origin of vein 3 to just below vein 2. The average total expanse of males of *A. fimbriata* is 27 mm ($n = 33$), females 29 mm ($n = 22$). The male genitalia are illustrated in Lindsey et al. (1931) as *Amblyscirtes bellus*.

Specimens Examined.—(33 males, 23 females). UNITED STATES. *New Mexico*: Sandoval Co., Jemez Springs, 14 Sept. 1914, 4 males, 5 females (J. Woodgate, AMNH). *Arizona*: Cochise Co., Chiricahua Mts., 21 June 1932, 1 male, 2 females (L. Hulbirt, HAF), 26 June 1936, 1 male (L. Hulbirt, HAF), 28 June 1942, 2 males, 4 females (L. Hulbirt, HAF); Ramsey Canyon, 28 June 1936, 2 males, 2 females (L. Hulbirt, HAF); Rustlers Park, 20 June 1963, 1 male (L. Freeman, HAF), 2 males (H. A. Freeman, HAF); Pinery Canyon, 6500 ft, 11 July 1960, 4 males, 5 females (H. A. Freeman, HAF), 1 female (H. A. Freeman, CMNH); Onion Saddle, 12 July 1960, 1 male, 2 females (H. A. Freeman, HAF); Portal, 10 July 1960, 1 female (H. A. Freeman, HAF). *MEXICO*. *Nuevo Leon*: Monterrey, Chipinque Mesa, 13 Aug. 1967, 1 male (AMNH); La Palma-Rayones, 4000 ft, 7 July 1990, 1 male (J. Kemner, HAF). *Coahuila*: 8 mi E Los Lirios, San Rafael 8200 ft, 7 June 1989, 2 males (J. Kemner, HAF). *Oaxaca*: Sierra Juarez, La Cumbre-El Punto, 9500 ft, 13 Apr. 1989, 1 male (J. Kemner, HAF), 1 male (J. Kemner, CMNH), 22 Apr. 1989, 3 males (J. Kemner, HAF), 24 Apr. 1989, 1 male (J. Kemner, HAF), 9 Apr. 1990, 1 male (J. Kemner, HAF); Sierra Juarez, 3 mi E La Trinidad, 20 May 1990, 1 male (J. Kemner, HAF); river 5 mi E Ixtlan de Juarez, 7500 ft, 20 May 1990, 1 male (J. Kemner, HAF); 1–5 mi E Ixtlan de Juarez, 7500 ft, 4 July 1991, 1 male (J. Kemner, HAF); 18 mi E Mitla, San Lorenzo, 16 June 1989, 2 males (J. Kemner, HAF).

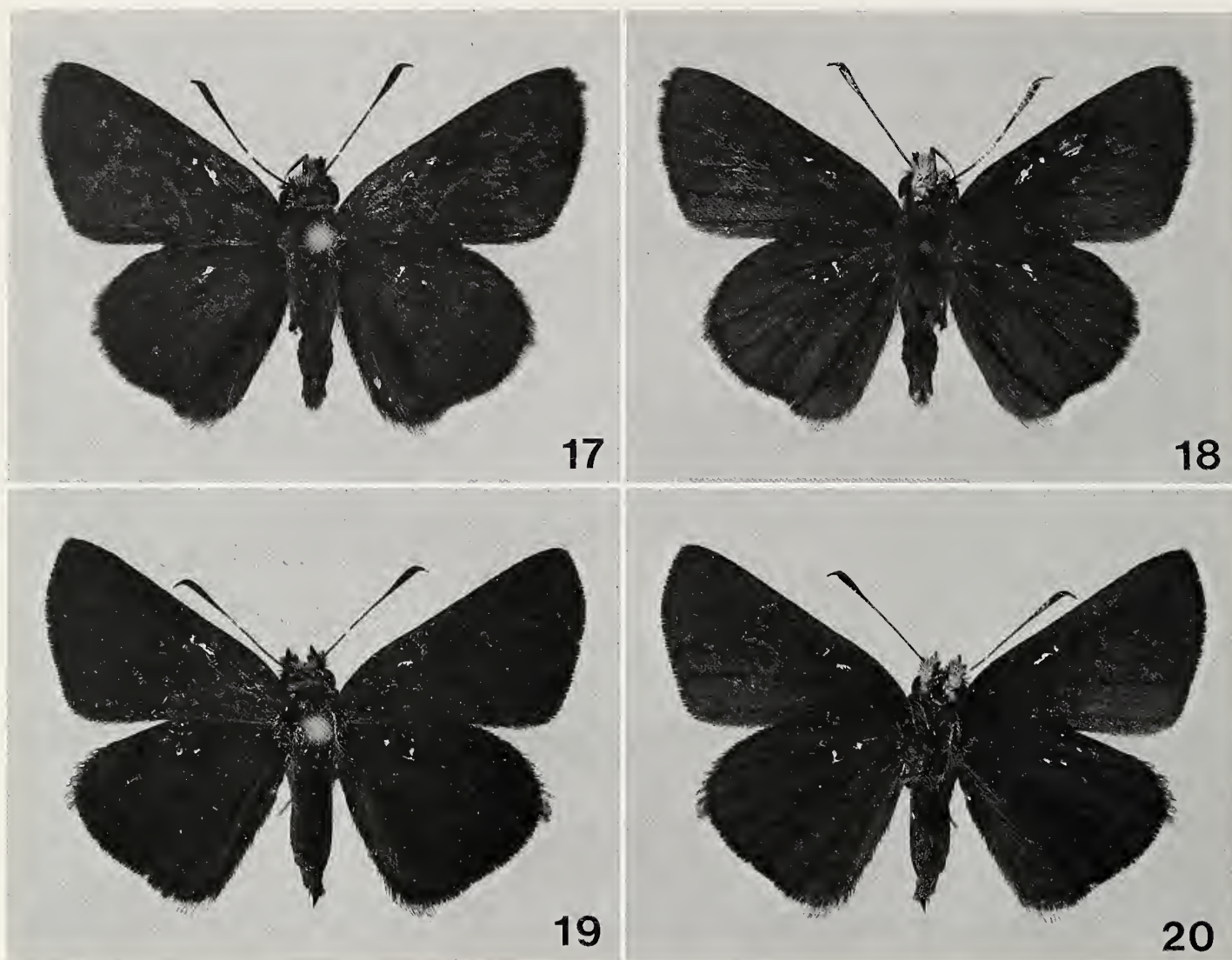


Fig. 17–20. — *Amblyscirtes fimbriata pallida* Freeman: 17, male holotype, upper surface from Mexico, Mexico, 64 km W Toluca, 9300 ft, 10 June 1989 (John Kemner); 18, lower surface of specimen in Fig. 17; 19, female paratype, upper surface, from Mexico, Mexico, 64 km W Toluca, 9300 ft, 10 June 1989 (John Kemner); 20, lower surface of specimen in Fig. 19.

Discussion. — *Amblyscirtes f. fimbriata* occurs commonly in Arizona and New Mexico and extends to Oaxaca, Mexico, at fairly high elevations. Specimens of this subspecies collected at the Mexican localities mentioned above are the same as ones found in Arizona and New Mexico in size and general appearance.

Amblyscirtes fimbriata pallida Freeman, **new subspecies**
(Fig. 17–20)

Type Locality. — MEXICO. Mexico: 64 km W Toluca, 9300 ft.

Diagnosis. — This subspecies differs from *A. fimbriata fimbriata* in having the fringes of both wings in both sexes snow white to very pale yellow, never orange. Some specimens look very similar to *Amblyscirtes phylace*, however the orange head and palpi of females and the long, narrow gray stigma extending from the origin of vein 3 to vein 1 in the males in *A. fimbriata pallida* easily separate the two species. The fringe coloration and slightly smaller total expanse are the only differences between *A. fimbriata pallida* and *A. fimbriata fimbriata*. Total expanse of males 24 mm ($n = 17$), females 26 mm ($n = 35$). The genitalia are the same as *A. f. fimbriata*.

Discussion. — The entire type series was collected on 10 June 1989 by John

Kemner. Most of the males were “puddling” or found near moist spots, and the females were “nectaring” on small white flowers. So far this subspecies has not been collected at any other location.

Type Material. — Holotype: male *Amblyscirtes fimbriata pallida* Freeman; MEXICO. Mexico, 64 km W Toluca, 9300 ft, 100 June 1989, John Kemner; length of fore wing 13.4 mm, length of hind wing, 10.4 mm; deposited in CMNH. There are 16 male and 34 female paratypes, same data as holotype, in my collection (HAF) and one female paratype in the CMNH at the present time. Paratypes will be placed in the following museums: CMNH, AMNH, USNM, and AME.

CHECKLIST OF THE GENUS *AMBLYSCIRTES*

This checklist includes the presently known species and subspecies of *Amblyscirtes* and synonyms.

vialis (W. H. Edwards, 1862)
asella (Herrich-Schäffer, 1869)
linda Freeman, 1943
fluonia Godman, 1900
aenus W. H. Edwards, 1878
erna Freeman, 1943
cassus W. H. Edwards, 1883
texanae Bell, 1927
hegon (Scudder, 1863)
samoset (Scudder, 1863)
nemoris (W. H. Edwards, 1864)
argina (Plötz, 1884)
carolina Skinner, 1892
reversa Jones, 1926
aesculapius (Fabricius, 1793)
textor (Geyer, 1831)
oneko (Scudder, 1863)
wakulla (W. H. Edwards, 1869)
nereus (W. H. Edwards, 1876)
nysa (W. H. Edwards, 1877)
similis (Strecker, 1878)
eos (W. H. Edwards, 1871)
comus (W. H. Edwards, 1876)
nilus (W. H. Edwards, 1878)
quinquemacula (Skinner, 1911)
elissa elissa Godman, 1900
elissa arizonae Freeman, 1993
alternata (Grote and Robinson, 1867)
meridionalis Dyar, 1905
tolteca tolteca Scudder, 1872
tolteca prenda Evans, 1955
celia Skinner, 1895
belli Freeman, 1941
oslari Skinner, 1899
brocki Freeman, 1991
exoteria (Herrich-Schäffer, 1869)

nanno W. H. Edwards, 1882
marcus (Strand, 1907)
folia Godman, 1900
tutolia Dyar, 1913
raphaeli Freeman, 1973
immaculatus Freeman, 1970
patriciae (Bell, 1959)
phylace (W. H. Edwards, 1878)
anubis (Godman, 1900)
fimbriata fimbriata (Plötz, 1882)
bellus (W. H. Edwards, 1884)
fimbriata pallida Freeman, 1993

Three species that were previously recorded by Evans (1955) and Freeman (1973) as being members of the *Amblyscirtes* (*Amblyscirtes simius* W. H. Edwards, 1881, *Amblyscirtes insulaepinorum* Holland, 1916, and *Stomyles florus* Godman, 1900) are not included in the checklist because they are not members of the genus *Amblyscirtes*. None of these species have the basic characteristics of the genitalia of the 28 species of *Amblyscirtes* listed, which have a long aedeagus with the terminal end divided, a long narrow saccus, and the tegumen with a delicate, middorsal, caudally arching prong over a somewhat oval opening. The correct generic placement of these three species, based on their genitalia and some other features, awaits further study.

ACKNOWLEDGMENTS

I thank Dr. J. E. Rawlins (CMNH) for making the photographs used in this article, for loaning specimens for study, and for offering helpful suggestions; Dr. J. M. Burns (USNM) for helpful suggestions and the loan of specimens; J. Kemner, Dripping Springs, Texas, for collecting many of the specimens used in this study; J. P. Brock (JPB) and D. D. Mullins, Tucson, Arizona, for furnishing specimens from Arizona and the Sonoran Desert.

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EXCEPTIONAL NEW DENTITIONS OF THE DIMINUTIVE
PLESIADAPIFORMS *TINIMOMYS* AND *NIPTOMOMYS* (MAMMALIA),
WITH COMMENTS ON THE UPPER INCISORS OF
PLESIADAPIFORMES

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ABSTRACT

Complete lower and nearly complete upper dentitions of the micromomyid *Tinimomys graybulliensis* and a nearly complete lower dentition of the microsyopid *Niptomomys doreenae* are illustrated, and previously unknown teeth are described. Both specimens are from the lower Willwood Formation (early Wasatchian) of the Bighorn Basin, Wyoming. The first known I¹⁻² of *T. graybulliensis* provides the stimulus for broader comparison of the specialized upper central incisors of plesiadapiforms. Plesiadapids, paromomyids, saxonellids, and carpolestids have more or less similar, multicusped I's, supporting close relationship of these families. I¹ structure suggests that micromomyids are more distantly related (although postcranial evidence suggests that they may be closer to Paromomyidae). None of these plesiadapiform upper incisors shows any particular resemblance to those of euprimates. Based on incisor form, Microsyopidae are likely to be only distantly related to plesiadapiforms.

INTRODUCTION

The Clarkforkian-early Wasatchian plesiadapiforms *Tinimomys graybulliensis* and *Niptomomys doreenae* are among the smallest species that have been referred to the Primates, each probably weighing less than 35 g (see Conroy, 1987; Fleagle, 1988; and below for body weight estimates). With molars on the order of 1 mm long, their cheek teeth are substantially smaller than those of any extant primate (cf. Swindler, 1976), rivalling those of shrews (cf. Repenning, 1967) in their diminutive size.

Tinimomys represents the family Micromomyidae, and *Niptomomys* belongs to the uintasoricine Microsyopidae. While these assignments are relatively well established, the precise phylogenetic position of both families within Plesiadapiformes, and even their allocation to this suborder, are uncertain. For example, Szalay and Delson (1979) included *Tinimomys* in the plesiadapiform family Paromomyidae, but excluded Microsyopidae (including *Niptomomys*) from Plesiadapiformes and Primates. Hoffstetter (1988) followed Szalay and Delson concerning Microsyopidae, and even questioned the plesiadapiform status of

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Tinimomys. Gunnell (1989), however, included both of these genera in the Microsyopidae, within the suborder Plesiadapiformes, which he retained in the Primates with a query.

The primate status of Plesiadapiformes as a whole also has been seriously questioned in recent years (e.g., Martin, 1986, 1990; Gingerich, 1989; Gunnell, 1989; Beard, 1990, 1991, 1993; Kay et al., 1990, 1992), although nearly all studies agree that they are closely related to undoubted primates. Beard (1990, 1991, 1993) presented postcranial and other evidence that most taxa conventionally included in Plesiadapiformes are closer to Dermoptera (otherwise consisting of only the extant *Cynocephalus*) than to Primates, and he expanded the Dermoptera to include these plesiadapiforms. He further proposed that Dermoptera is the probable sister group of Primates (i.e., Euprimates). Kay et al. (1990, 1992) documented cranial characters that support a close alliance between plesiadapiforms and Dermoptera, but their analysis led to the conclusion that Scandentia rather than Plesiadapiformes is the sister group of Primates.

Resolution of these controversies is obviously beyond the realm of this note. For convenience, however, we refer herein to *Tinimomys* and *Niptomomys* as plesiadapiforms.

Early Wasatchian specimens of the plesiadapiforms *Tinimomys graybulliensis* and *Niptomomys doreenae* recently discovered in the lower Willwood Formation of the Bighorn Basin, Wyoming, are the most complete known dentitions of these species and provide previously unknown information about the antemolar dentitions. Although both of these species have become better known in recent years (e.g., Bown, 1979; Rose and Bown, 1982; Beard and Houde, 1989; Gunnell, 1989), they are still among the rarest elements of early Eocene mammalian faunas. The purpose of this note is to put on record the anatomy of these exceptional new specimens which, in the case of *Tinimomys*, contributes new information bearing on its phylogenetic position.

Abbreviations are as follows: a, anterocone; l, laterocone; lc, lateroconule; m, mediocone; mc, mediocrista; p, posterocone. Institutional acronyms are: AMNH, American Museum of Natural History, New York; AV, Muséum National d'Histoire Naturelle, Paris; PAT, Laboratoire de Paléontologie, Montpellier, France; UA, University of Alberta, Edmonton; UM, University of Michigan, Ann Arbor; USGS, U.S. Geological Survey, Denver; USNM, National Museum of Natural History, Washington, D.C.; UW, University of Wyoming, Laramie; Wa, Geologisch-Paläontologisches Institut, Halle, Germany.

SYSTEMATIC PALEONTOLOGY

Family Microsyopidae Osborn and Wortman, 1892

Niptomomys doreenae McKenna, 1960

A nearly complete right dentary of this species (USGS 25496; Fig. 1) was collected in 1992 by Suzanne Strait from very low in the Willwood Formation (UW locality V-73037, approximately 5 miles east of Worland, Washakie County, Wyoming; 34-m level; see Bown, 1979). It preserves P_3 - M_3 , the bases of two anterior teeth, and an alveolus between them and P_3 . The two anterior teeth, the first enlarged and the second vestigial, have been interpreted as I_1 and the canine, giving a lower dental formula of 1-1-3-3 (Bown and Gingerich, 1972). However, the close proximity and small size of the second tooth, and the slightly larger size of the third tooth (as suggested by its alveolus), leave open the possibility that

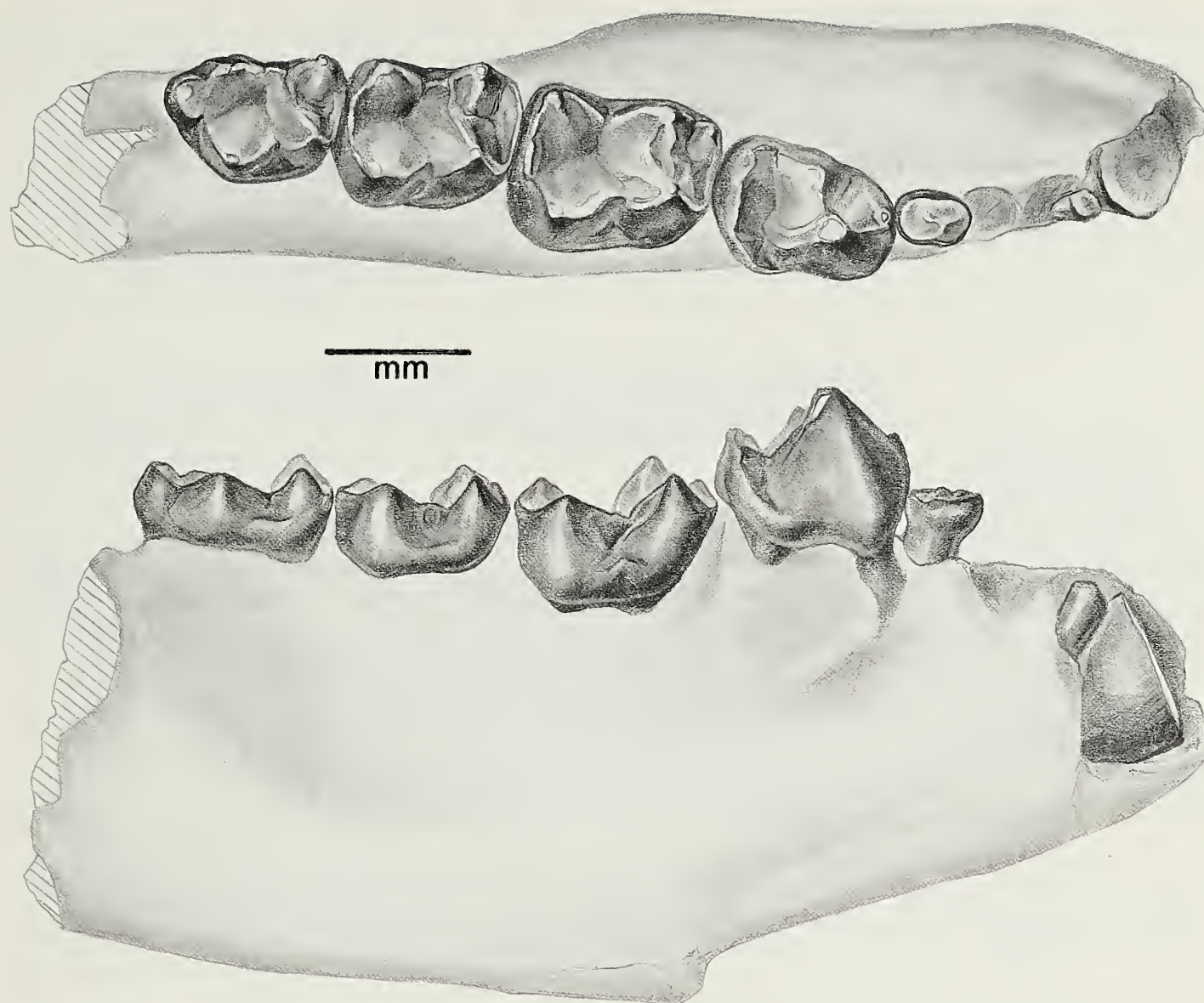


Fig. 1.—*Niptomomys doreenae*, USGS 25496, right dentary with P_3 – M_3 and bases of I_1 and ?C; occlusal and lateral views. Scale is 1 mm.

the lower dental formula could be 2-1-2-3 or even 2-0-3-3. The lower dentition of this species has been adequately described by McKenna (1960), Szalay (1969*b*), and Bown (1979).

Measurements (mm) of USGS 25496 are: P_3 length = 0.5, breadth = 0.4; P_4 L = 1.25, B = 0.95; M_1 L = 1.35, B = 1.15; M_2 L = 1.20, B = 1.00; M_3 L = 1.25, B = 0.85.

Family Micromomyidae Szalay, 1974
Tinimomys graybulliensis Szalay, 1974

Associated lower and upper dentitions (USNM 461201, Fig. 2) of this diminutive species were extracted by acid preparation from a nodule collected in the Willwood Formation of the Clark's Fork Basin, Wyoming (approximately UM locality SC-26, sec. 4, T. 55 N., R. 101 W., Park County, Wyoming; early Wasatchian; see Rose, 1981; Gingerich and Klitz, 1985; Houde and Olson, 1992). The right dentary is complete except for the top of the coronoid process, and contains its full complement of seven teeth. The lower dental formula has been interpreted to be 1-0-3-3 (Bown and Rose, 1976; Beard and Houde, 1989; Gunnell, 1989), but there is, in fact, little direct evidence for this interpretation and it could as well be 1-1-2-3, or even 2-0-2-3. A palatal fragment contains the right P^2 – M^3 .

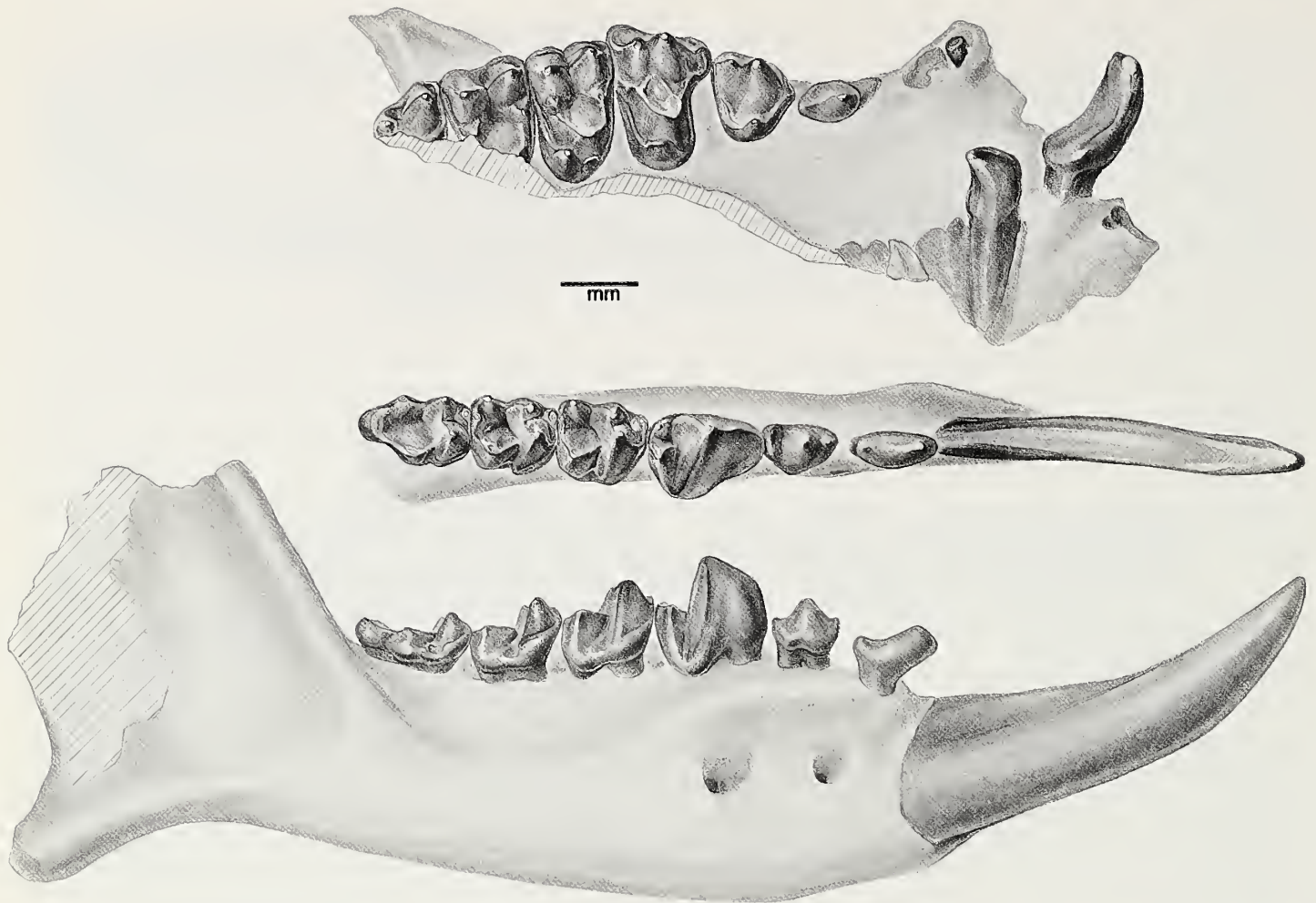


Fig. 2.—*Tinimomys graybulliensis*, USNM 461201. Top: Fragmentary palate with right P²–M³ (M²⁻³ incomplete lingually) and left I¹⁻². Center and bottom: Right dentary with complete dentition, in occlusal and lateral views. Scale is 1 mm.

Anterior to P² and separated by a short diastema are two alveoli (the anterior one containing a small root), evidently for a two-rooted canine or P¹. Attached to the palate is a left premaxillary fragment with two incisors, which has been displaced posteriorly. The teeth are interpreted as I¹⁻² because the anteriormost is larger and broader and has accessory cuspules besides its apical cusp (as is typical of the central incisor in plesiadapiforms; a mesial contact facet cannot be discerned); whereas the second tooth is laterally compressed and simple, resembling I² in *Ignacius* and *Nannodectes*. Isolated right I¹⁻² are also preserved.

P₃–M₃ and P³–M³ have been figured and described previously (e.g., Szalay, 1974; Bown and Rose, 1976; Gunnell, 1989; Beard and Houde, 1989). The elongate, laterally compressed lower incisor, as observed by Beard and Houde (1989), more closely resembles that of *Saxonella* than of any other plesiadapiform. The second tooth (P₂?) has an elongate crown, which projects anteriorly over its single root. It is a simple tooth with a large anteriorly placed protoconid followed by a low talonid cusp. P² is also simple but two-rooted, longer than wide, and has an anteriorly situated apical cusp and a faint lingual cingulum. I² is simple, laterally compressed, with a slightly recurved tip. Its crown is about three-fourths as high as that of I¹. The central incisor is robust at its base, about twice as deep labiolingually as it is in transverse diameter. In lateral profile the crown is hook-shaped. It is dominated by a large, somewhat laterally situated apical cusp (presumably homologous with the anterocone of plesiadapids) separated by a shallow furrow from a much smaller and lower medial cusp (mediocone). The basolingual border

of the right I¹ is faintly swollen in the position of a posterocone, but this can barely be discerned on left I¹. Basolaterally is a weakly formed cusp here termed a *lateroconule* rather than a laterocone, because it is basal rather than apical; a true laterocone appears to be absent. Comparison of this distinctive I¹ with those of other plesiadapiforms affords new evidence on the affinities of *Tinimomys*.

Measurements (mm) of USNM 461201 are: P₂ or C length = 1.05, breadth = 0.50; P₃ L = 0.95, B = 0.65; P₄ L = 1.40, B = 1.10; M₁ L = 1.20, B = 1.10; M₂ L = 1.10, B = 0.95; M₃ L = 1.45, B = 0.90; P² L = 0.80, B = 0.50; P³ L = 1.10, B = 1.15; P⁴ L = 1.35, B = 1.80; M¹ L = 1.10, B = 1.70; M² L = 1.05.

UPPER INCISORS OF PLESIADAPIFORMS

The upper central incisors of many plesiadapiforms are easily recognized by their distinctive multipronged “mitten-shaped” crowns. Although this characteristic structure has long been known (e.g., Matthew, 1917; Gidley, 1923), surprisingly few specimens have been found that preserve serially associated upper incisors with complete crowns in the same jaw with cheek teeth; most upper incisors that have been allocated to various plesiadapiform species are isolated. Besides *Tinimomys* described here, serially associated upper central incisors have been illustrated or described only in the plesiadapids *Nannodectes* (Matthew, 1917; Simpson, 1935; Gingerich et al., 1983) and *Plesiadapis* (Russell, 1967; Gingerich, 1976), the carpolestid *Carpolestes* (Gingerich, 1987), the paromomyid *Arcius* (Godinot, 1984), and the microsyopids *Microsyops* (Gunnell, 1989) and *Megadelphus* (Szalay, 1969a; Gunnell, 1989)—and for only a single specimen of each except in the case of *Nannodectes* and *Arcius*, where there are two. Incisors have been reported for several other plesiadapiform genera, but taxonomic allocations have been based on presumed association, size, or morphology consistent with the incisors of taxa listed above, and they remain to be corroborated.

Incisors of various plesiadapiforms are illustrated in Fig. 3. It is evident that the incisors of plesiadapids (Fig. 3C), paromomyids (Fig. 3D–H), saxonellids (Fig. 3J), and carpolestids (Fig. 3K) are variations on a similar theme, and the probable specialized nature of this structure is further evidence of the close relationship among these plesiadapiform families. I¹ in members of all these families is characterized by a prominent anterocone (usually the largest cusp), a large laterocone, a variably developed mediocone (absent in at least some carpolestids and paromomyids), and a distinct posterocone (again of variable expression). The mediocone is situated more proximally in plesiadapids than in other plesiadapiforms (about even with the laterocone), and it is possible that not all mediocones are homologous.

Plesiadapid I¹s (except *Platychoerops*, which was apparently further modified: Gingerich, 1976:fig. 26) always have the anterocone as the largest cusp, with the laterocone typically large as well, except in the most derived species in which the laterocone may be reduced (Gingerich, 1976; Krause, 1978:fig. 4, 10; Hooker, 1991:fig. 1). The posterocone is also well-developed, whereas the mediocone tends to be much smaller and lower than the anterocone. A weak centroconule is present between the mediocone and laterocone in some later species (e.g., *Plesiadapis rex*, *P. churchilli*, *P. tricuspis*: Gingerich, 1976; Krause, 1978). In *Nannodectes gidleyi* (Fig. 3C) there is a basolateral accessory cusp (termed here the lateroconule and in the same position as that of *Tinimomys*) between the laterocone and the base of the crown. A similar, possibly homologous cusp occurs in two other incisor morphs discussed below (Fig. 3B, 3L) as well as *Tinimomys*.

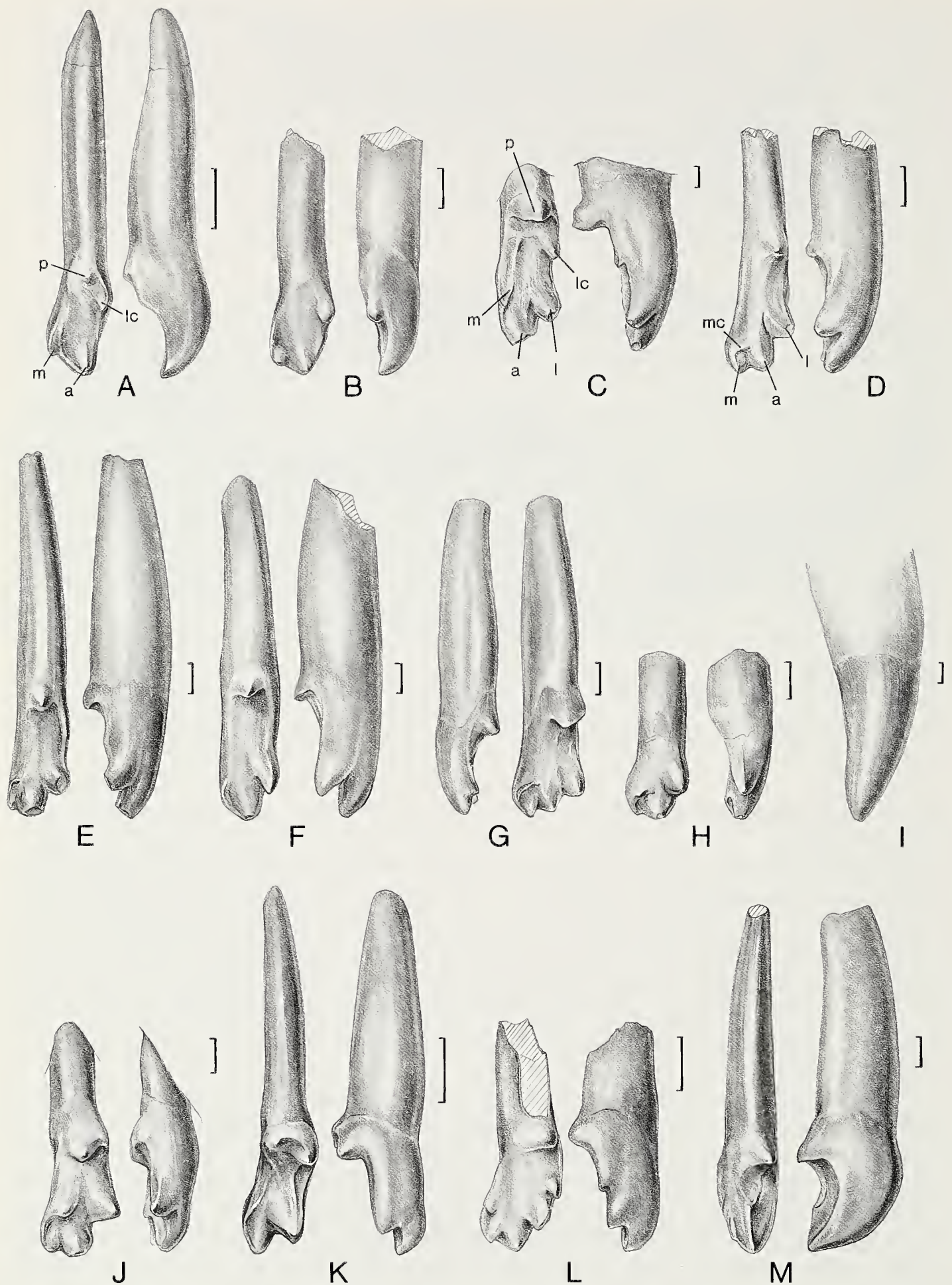


Fig. 3.—Right upper central incisors of plesiadapiforms and related forms, in lingual and lateral views unless otherwise noted. A, *Tinimomys graybulliensis*, USNM 461201; B, Unidentified left incisor (reversed), possibly *Palaechthon alticuspis*, USNM 10090, partly restored from USNM 10010 (Torrejonian); C, *Nannodectes gidleyi*, AMNH 17171 (Tiffanian); D, *Phenacolemur simonsi*, USGS 9620 (early Wasatchian); E, *Phenacolemur* cf. *pagei*, USGS 2216 (late Clarkforkian); F, *Phenacolemur* sp.,

In presumed paromomyid I's the anterocone and laterocone are typically well-developed and the posterocone is usually somewhat smaller, but the mediocone is quite variable. The mediocone is nearly as big and as distal as the anterocone in early Wasatchian *Phenacolemur simonsi* (Fig. 3D), but much smaller and slightly more proximal in Clarkforkian *P. pagei* (Fig. 3E). In both of these, a short crest ("mediocrista") curves proximolaterad from the mediocone. I' in middle Wasatchian *Phenacolemur* sp. (Fig. 3F) has only a slightly less curved mediocrista but no distinct mediocone. In contrast, the mediocone of *Arcius lapparenti* (Fig. 3G) is the most distal cusp and is only slightly smaller than the subequal anterocone and laterocone, giving the apex a broad, serrate margin. A mediocrista is present and the posterocone is very large. *A. rougieri* (Fig. 3H) differs markedly in having the anterocone decidedly the largest cusp, the laterocone conspicuously more proximal, and the mediocone and posterocone nearly absent; again a distinct mediocrista is present. The differences between the I's of the two *Arcius* species when compared with other plesiadapiforms raise the question whether these two species should be included in the same genus.

Isolated upper incisors from the Thanetian of Walbeck, Germany, have been attributed to *Saxonella crepaturae* (Fig. 3J; see Russell, 1964:plate 8, fig. 6d). They are very similar to those of *Phenacolemur* (which is not known from the site), but have slightly stronger laterocone and posterocone and a small cusplule present on the mediocrista. The close correspondence to paromomyid incisors suggests that Saxonellidae could be more closely related to Paromomyidae than to any other plesiadapiform family (see also Gingerich, 1976), although this is not particularly supported by other aspects of the dentition (Rose, 1975; Fox, 1991).

An associated I' of a carpolestid (*Carpolestes nigridentis*, the most derived and youngest species) has recently been illustrated (Gingerich, 1987:fig. 6) but not described. From the published figure it appears to differ from other plesiadapiforms (including putative carpolestid I's), but resembles *Tinimomys*, in lacking a laterocone. Isolated I's referred to *Carpodaptes cygneus* (Fig. 3K; see Krause, 1978), however, are distinctive in having a very strong laterocone, even larger than the anterocone, a low crest mesioproximal to the anterocone but no mediocone, and a double posterocone, the lateral cusp substantially larger. An isolated I' identified as ?*Carpodaptes hazelae* by Fox (1984:fig. 6), judging from his figure, is similar to I' of *C. cygneus* but higher crowned and appears to have a small mediocone.

Two other previously illustrated isolated incisors are of interest and might belong to carpolestids. A tiny I' (USNM 9928, Fig. 3L) from the middle Paleocene Gidley Quarry ascribed by Gidley (1923:plate 3, fig. 10) to cf. *Palaechthon minor* (= *Palenochtha minor*) is strongly suggestive of incisors of plesiadapiforms and resembles I's of paromomyids and plesiadapids in particular. Like those, it has

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USGS 27405 (middle Wasatchian); G, *Arcius lapparenti*, AV 7714, medial and lingual views (Ypresian; after Godinot, 1984); H, *Arcius rougieri*, PAT 1 (Ypresian; after Godinot, 1984, and a cast of PAT 1); I, *Megadelphus lundeliusi*, AMNH 55284, lateral view (late Wasatchian; root restored from *Microsypops latidens*, USNM 19319; modified after Szalay, 1969a); J, *Saxonella crepaturae*, Wa/393 (Thanetian); K, *Carpodaptes cygneus*, UA 11088 (late Tiffanian); L, Unidentified incisor, probably either *Elphidotarsius florencae* or *Palenochtha minor*, USNM 9928 (Torrejonian); M, ?*Apatemys* sp., USGS 2460 (early Wasatchian). Scales are 1 mm.

a well-developed anterocone, laterocone, mediocone, and posterocone. The first three cusps are subequal in size. In addition, however, there is a small cuspule at the base of the mediocone ("medioconule") and a small but distinct lateroconule. The incisor is too small to belong to any known Gidley Quarry plesiadapiform besides *P. minor* or *Elphidotarsius florencae*. Although it is not possible at present to determine which (if either) of these species this incisor represents, the possibility that it may belong to *Elphidotarsius* should not be overlooked. Simpson (1928: fig. 13) depicted an incisor (AMNH 22169) from the Clarkforkian Bear Creek locality, which appears from his drawing to have a similar cusp arrangement, except for a double lateroconule. It is tempting to conclude that, if the Gidley Quarry incisor pertains to *Elphidotarsius*, the Bear Creek incisor could belong to the derived carpolestid *Carpolestes nigridentis*. However, both incisors are more elaborate than others that have been referred to carpolestids, and the Bear Creek specimen appears to differ significantly from the incisor of *Carpolestes nigridentis* illustrated by Gingerich (1987).

This raises the alternative that both of these incisors might instead belong to nonplesiadapiforms. The best candidates in that case are erinaceid or nyctitheriid insectivores, or plagiomenids, one or more of which are recorded from Gidley Quarry and Bear Creek, and all of which are known to have had multilobed lower incisors (e.g., Rose, 1973; Schwartz and Krishtalka, 1976; Sigé, 1976). Undescribed upper incisors from the Eocene of Ellesmere Island (in the Carnegie Museum collection), probably attributable to plagiomenids, closely resemble Simpson's Bear Creek incisor.

There is general agreement that the families discussed above are plesiadapiforms. More controversial is the Microsyopidae sensu stricto (i.e., not including Paleocene Palaechthonidae; see Gunnell, 1989). Since they have been considered plesiadapiforms by some workers (e.g., Bown and Rose, 1976; Gingerich, 1989; Gunnell, 1989), we include them here. Serially associated I's have been reported in early Bridgerian *Megadelphus lundeliusi* (Fig. 3I; see Szalay, 1969a:plates 50 and 52; Gunnell, 1989:fig. 49) and later Wasatchian *Microsyops latidentis* (Gunnell, 1989:fig. 36, 48). The latter specimen is damaged at the tip, and it is possible that it is I² rather than I¹. Szalay (1969a:plate 36) also allocated an isolated incisor (USNM 19319) to *M. latidentis*. It is noteworthy that all of these incisors are simple, conical or laterally compressed, and caniniform. They are very different from the multicusped incisors of plesiadapiforms, including *Tinimomys*. This structure does not provide support for close relationship of Microsyopidae with any known plesiadapiforms.

The isolation of *Tinimomys* relative to other genera conventionally considered plesiadapiforms is enhanced by the structure of its I¹ (Fig. 3A). In contrast to other plesiadapiforms, the posterocone in *Tinimomys* is weaker, and there is no laterocone. Moreover, the crown of I¹ in *Tinimomys* is relatively shorter than in most other plesiadapiforms, and in lateral perspective the tooth is more hook-shaped. In this regard it is more like the I¹ that has been referred to *Microsyops* (e.g., Gingerich, 1976:fig. 38; Bown, 1979:fig. 44e) but which belongs to almost certainly *Apatemys* (Fig. 3M; see Gingerich and Rose, 1982:fig. 1B); however, there is little other specific resemblance to apatemyids.

Probably the closest similarity to I¹ of *Tinimomys* is seen in isolated incisors from Gidley Quarry (USNM 10010 and 10090, Fig. 3B) identified by Gidley (1923:plate 3, fig. 8–9) as cf. *Pronothodectes* species. Like I¹ of *Tinimomys*, these incisors have relatively short crowns, an indistinct posterocone, and apparently a basal lateroconule (somewhat larger than in *Tinimomys*), but no laterocone.

They are less hook-shaped and have larger, more apical mediocones than in *Tinimomys*. These teeth are structurally unlike plesiadapid incisors and are probably too small to represent *Pronothodectes* anyway. Their size is most appropriate to belong to either *Paromomys depressidens* or *Palaechthon alticuspis* among Gidley Quarry plesiadapiforms and, because they also differ markedly from known paromomyid incisors, it is probable that they represent *Palaechthon*. (It is also possible, but we think less likely, that they do not belong to a plesiadapiform.) If our assignment is correct, the resemblance between these incisors and those of *Tinimomys* could be interpreted as evidence of a closer relationship between micromomyids and palaechthonids than between micromomyids and any other plesiadapiform family. However, because these incisors are simpler than those of other plesiadapiforms, the similarities could be largely or entirely plesiomorphous, indicating only that both families branched early from the plesiadapiform stem and retained the primitive incisor form. In this regard it is notable that recently discovered postcranial specimens of *T. graybulliensis* show derived resemblances to paromomyids and suggest a close relationship between micromomyids and paromomyids (Beard, in press).

COMMENT ON BODY-WEIGHT ESTIMATES

Weight estimates for these tiny mammals vary considerably depending on the regression equation used and the set of mammals selected to construct the equations. Conroy (1987) employed regressions based on lower molar size and body weight in extant primates to derive a weight estimate for *Tinimomys graybulliensis*, but inadvertent use of M_1 area rather than the natural logarithm of its area resulted in obvious overestimates of 81 g (prosimian equation) and 86 g (all-primate equation). Applying Conroy's equations to the measurements of M_1 by Bown and Rose (1976) and Beard and Houde (1989) (which are in close agreement, with mean M_1 areas of 1.07 and 1.10, and $\ln M_1$ areas of 0.07 and 0.10, respectively) the estimated mean body weight for *Tinimomys* should have been 16–17 g (prosimian equation) or 14–15 g (all-primate equation), much smaller than any extant primate. The equation of Gingerich et al. (1982), derived from the relationship between M_1 area and body mass in extant generalized primates, provides an estimate of 39–41 g. The same equations yield a weight of 21–23 g or 53 g, respectively, for the new specimen of *Tinimomys* described here. For the individual of *Niptomomys* described above we estimate the body weight to have been either 28–29 g or 68 g using these regressions.

As observed by Gingerich et al. (1982; see also Gingerich and Smith, 1984), living insectivores and insectivorous primates such as *Tarsius* have relatively large teeth compared to body mass and, therefore, smaller body weights than would be predicted using their generalized primate regression. In view of the dental anatomy of these two fossil genera (particularly *Tinimomys*) and their very small tooth size, their body weights were almost certainly at the lower end of the predictions above, and probably more consistent with those of insectivores than of primates. Living insectivores (soricids) with molar sizes comparable to *Tinimomys* typically weigh less than 10 g (see Gingerich and Smith, 1984:fig. 5).

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ERRATA

Volume 62, number 3, page 215. McCarthy et al., table 1: *Balantiopteryx io* (E) is indicated (X) as found in Nicaragua (Nic) while *Centronycteris maximiliani* is not. These are incorrect and should be reversed.

Volume 62, number 3, page 271. Erratum: The volume number for Vogt, R. C. (1993) is 62(1):1–46, not 61(1):1–46.

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